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REMARKS ON THE CLASSIFICATION OF THE *RUBIACEAE*

BY

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LIST OF CONTENTS

Preface 210

I. Historical introduction.

A. Older works. Classifications of De Candolle, Hooker, Bentham and Hooker, Baillon and K. Schumann 210

B. Recent work. Modifications of Bremekamp and others 213

II. Criticisms of the classifications proposed by previous authors . . . 217

III. The available criteria and their discussion.

A. List of the characters 221

B. Discussion of the characters 221

IV. Improvements which may be made to the classification. Position of Gaertnera and Henriquezieae. Division into subfamilies. Content of the subfamilies and tribes. Tabular exposition of proposed new classification 238

V. Phylogenetic considerations. Geographical distribution. Use of criteria of primitiveness 253

Bibliography 259

Appendix 1. Tables of the results of the examination of pollen, hairs, etc. from certain genera representative of all the tribes 261

Appendix 2. Bremekamp's latest views and validification of new names . 280

Plates VIII - XVI 282

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Preface.

A brief history of the attempts to classify the *Rubiaceae* is given and recently proposed characters are discussed. Hair and pollen characters have been examined in numerous genera representative of all the tribes which have ever been suggested. These and other characters are discussed. A new classification of the family is suggested.

Thanks are due to the Curators of the following herbaria: Missouri Botanical Gardens, Singapore Botanic Gardens, Calcutta Herbarium and the Royal Botanic Gardens, Kew, for the loan of extra-African material. The entire *Rubiaceae* preserved at Kew were examined during a brief period of leave in London. Since this thesis was prepared in Africa little could have been done concerning non-African genera without the help of these loans. Thanks are also due to my wife, Librarian of the East African Agriculture and Forestry Research Organisation for obtaining books not available in East Africa, to Messrs. J. P. M. Brenan of Kew and H. K. Airy Shaw, and to my tutor Prof. Harris for many suggestions.

I. — Historical Introduction.

A) *Older works.*

The family *Rubiaceae* is a very well-defined group and its members are readily recognised. The combination of simple opposite leaves and stipules is the most obvious diagnostic character. Only a very few genera are doubtfully placed and sometimes placed in other families.

The most recent general account of this large and widely distributed family is that of Karl Schumann (1891). This will long continue to be of great practical value but recent work shows that the classification which he employs is in need of modification. Schumann's classification differs but little from those of earlier authors, save of course for the inclusion of numerous newly described genera. A. Richard (1830) was the first person to write a monograph dealing with the family though even this was based on the work of De Candolle and Jussieu. This very early work need not be discussed and the first classification having influence on modern work is that of De Candolle (1830). He divides the family up as follows:

Locules of ovary with one ovule :	Locules of ovary with many ovules (two or more) :
Cordiereae	
Guettardaceae	*Cinchonaceae*
Paederieae	*Gardeniaceae*
Coffeaceae	*Hedyotideae*
Spermacoceae	*Isertieae*
Anthospermeae	*Hamelieae*
Stellatae	
Opercularieae	

Several of these tribes are subdivided. Bentham in Hooker (1849) suggested several changes which mostly concerned the moving of certain genera from one tribe to another and altering tribe names. The *Hamelieae* were to be suppressed, the *Rondeletieae* raised to tribal status, and the *Guettardeae* and *Coffeeae* merged into one tribe with 4-5 subtribes (including *Vanguerieae, Guettardeae, Ixoreae,* and *Psychotrieae).*

A large number of new *Rubiaceae* were discovered in the next 25 years and Bentham and Hooker (1873) recognised 25 tribes divided into three series based on the number of ovules :

Series A : Ovules in the locules almost always indefinite in number : *Naucleeae, Cinchoneae, Henriquezieae, Condamineeae, Rondeletieae, Hedyotideae, Mussaendeae, Hamelieae, Catesbaeeae, Gardenieae.*

Series B : Ovules paired, collateral in each locule : *Cruckshanksieae, Retiniphylleae.*

Series C : Ovules solitary in the locules : *Guettardeae, Knoxieae, Chiococceae, Alberteae, Vanguerieae, Ixoreae, Morindeae, Coussareeae, Psychotrieae, Paederieae, Anthospermeae, Spermacoceae* and *Galieae.*

This system was followed by the writers of floras and others during the next 25 years and only small modifications were suggested. Hiern (1877) indicates that the *Knoxieae* are better placed in the *Vanguerieae* in his opinion. Sonder (1865) on the other hand includes the *Knoxieae* with the *Spermacoceae* and divides the *Vanguerieae* between the *Guettardeae* and *Coffeeae* (= *Ixoreae*).

Baillon monographed the *Rubiaceae* in Tome 7 of his «Histoire des Plantes» (1880). He recognised only 15 tribes and considered that the *Caprifoliaceae* (including *Adoxaceae* in those days) should not be separated from the *Rubiaceae.* Although this classification was never accepted there are several points worthy of mention. He transferred several genera from the *Cinchoneae* to the *Hedyotideae* thus anticipating very recent work, and renamed the *Galieae, Rubieae,* which is correct since *Rubia* is the type genus of the

family and of its tribe. The difference in his classification may be expressed by listing his tribes :

Rubieae, Spermacoceae, Anthospermeae, Coffeae, Uragogeae (= *Psychotrieae*), *Morindeae* (including *Guettardeae, Cruckshanksieae,* and *Retiniphylleae*), *Chiococceae* (including *Knoxieae, Alberteae,* and *Vanguerieae*), *Genipeae* (including *Gardenieae, Catesbaeeae,* and *Mussaendeae*), *Oldenlandieae* (= *Hedyotideeae* and including *Rondeletieae*), *Portlandieae* (= *Condamineeae*) and *Cinchoneae* (including *Naucleeae* and *Henriquezieae*).

K. Schumann (1891) recognised 21 tribes arranged in a very similar way to the system of Bentham and Hooker, the differences being of minor importance. The *Hedyotideae* are called *Oldenlandieae* and are made to include the *Cruckshanksieae*. The *Hamelieae, Catesbaeeae* and *Retiniphylleae* are merged with the *Gardenieae*. In general plan this classification is very similar to that of De Candolle and has been used by many writers of the present century.

During this century, however, many suggestions have been made in order to modify the old scheme. Mattei (1908) at the end of the description of a supposed new species of *Pentanisia* expressed doubt as to the validity of the ovule character of subdividing the family. He recognised the affinity (2) of the *Knoxieae* to the *Hedyotideae*.

Wernham (1912) in a series of papers on floral evolution of the *Sympetalae* made no changes in the accepted classification but suggested that the *Rubieae* should be considered a separate family thus following Lindley (1853). He upheld the theory that the *Rubiaceae* were derived from the same stock as the *Umbelliferae, Araliaceae,* and *Cornaceae* (vide chart on p. 230 of the reference). In 1916 he drew up a valuable key to the genera of Tropical American *Rubiaceae* but again did not depart from the usual classification. More will be said about the position of the *Rubieae* but it should be noted that if they were separated off as a separate family it would have to be called *Rubiaceae* and the remainder of the family *Cinchonaceae*. Rendle (1925) adopts Schumann's classification without any modifications. Hutchinson (1926) does not discuss the internal classification of the family. The first complete

(2) It may be pointed out here that when it is suggested that two genera or groups are related (either by myself or quoted from some other author) it means basically that they are morphologically similar over a large range of structures — there is scarcely ever any more concrete evidence to show that the two groups were derived from a fairly immediate common ancestor. In very many cases it is probable that morphology is an excellent pointer but the word « hypothetically » should be understood when « related » is used.

break-away from the old system was made by Hutchinson and Dalziel (1931) in their « Flora of West Tropical Africa ». The primary division of the family by means of the number of ovules is not followed but the groups are separated by means of the aestivation of the corolla lobes. The *Alberteae* come next to the *Gardenieae* and the *Knoxieae* are included in the *Hedyotideae* despite their having solitary ovules. The order of the tribes represented in West Africa is as follows : *Cinchoneae, Gardenieae, Alberteae, Ixoreae, Hamelieae, Naucleeae, Mussaendeae, Vanguerieae, Morindeae, Psychotrieae, Hedyotideae, Spermacoceae, Anthospermeae,* and *Galieae*. Moreover these authors clearly indicate that certain genera placed in different tribes are actually closely related (e. g. footnote on *Tarenna* and *Pavetta* on p. 75).

Mention should be made of a paper on the « Comparative Embryology of the *Rubiaceae* » by Lloyd (1899). In his preface he states that the investigation was undertaken with a view « to lead to a clearer understanding of the relationships between the genera of a very highly specialised and polymorphous family ». His studies covered 9 genera and he made no suggestions on relationships. One remark has a distinct bearing on the ovule character. The topographic relations of a placenta in *Houstonia (Hedyotideae)* and an ovule in the *Rubieae* are the same and no differences have been observed in their origin.

Before commencing a section on more recent work on the classification of the family a table p. 214 showing the various characters which have been used for the subdivision of the family in the past is given.

B) *Recent work.*

The most far-reaching changes have been made by Dr. C. E. B. Bremekamp in the introductory parts of several of his revisions of Rubiaceous groups. In 1934 he pointed out how related genera were dispersed over two quite separate tribes due to the use of the ovule character. This was not a new observation since Hutchinson and even Bentham and Hooker had indicated that the existing classification cut across certain affinities. Bremekamp removed a group of genera formerly placed in the *Gardenieae* (*Tricalysia, Tarenna,* etc,) and placed them in the *Ixoreae*. In the same paper he refutes the usefulness of the wing surrounding certain seeds as a character and separated *Crossopteryx* and

Table of the characters used for classification in the past.

	Ovules per loculus Number and position	Fruit	Aestivation of Corolla	Seeds	Radicle	Albumen	Stipules
Naucleeae	many (E)	caps.	not cont.	wing. (E)	sup.	pres.	entire (E)
Cinchoneae	many	caps.	various	wing.	sup.	pres.	entire (E)
Henriquezieae	many	caps.	imbr.	wing.	—	none	entire
Condamineeae	many	caps.	valv.	wing. (E)	—	pres.	entire (E)
Rondeletieae	many	caps.	not valv.	wing. (E)	—	pres.	entire (E)
Hedyotideae	many (E)	caps. (E)	valv.	exal. (E)	—	pres.	div. (E)
Mussaendeae	many	succ. (E)	valv.	exal.	—	pres.	entire (E)
Hamelieae	many	succ.	not valv.	exal.	—	pres.	entire
Catesbaeeae	many	succ.	valv.	exal.	—	pres.	entire
Gardenieae	many	succ.	not valv.	exal.	—	pres.	entire
Cruckshanksieae	2	caps.	valv.	exal.	inf.	pres.	entire
Retiniphylleae	2	succ.	cont.	exal.	—	pres.	entire
Guettardeae	1 desc.	succ.	not cont.	exal.	sup.	none	entire
Knoxieae	1 desc.	succ. (E)	valv.	exal.	sup.	pres.	div.
Chiococceae	1 desc.	succ. (E)	not cont.	exal.	sup.	pres.	entire
Alberteae	1 desc.	succ.	cont.	exal.	sup.	pres.	entire
Vanguerieae	1 desc.	succ.	valv.	exal.	sup.	pres.	entire
Ixoreae	1 various	succ.	cont.	exal.	inf.	pres.	entire
Morindeae	1 mid.	succ.	valv.	exal.	inf.	pres.	entire (E)
Coussareeae	1 erect	succ.	valv.	exal.	inf.	pres.	entire
Psychotrieae	1 erect	succ.	valv.	exal.	inf.	pres.	div. (E)
Paederieae	1 erect	caps. (E)	valv.	exal.	inf.	pres.	entire
Anthospermeae	1 erect	succ. (E)	valv.	exal.	inf.	pres.	entire (E)
Spermacoceae	1 mid.	caps. (E)	valv.	exal.	inf.	pres.	div. (E)
Galieae	1 mid.	succ.	valv.	exal.	inf.	pres.	foliar

ABBRIEVIATIONS.

E = indicates there are exceptions.
desc. = descending.
mid. = attached to middle of septum.
caps. = fruit a capsule.
succ. = fruit succulent OR dry but indehiscent.
valv. = valvate.
pres. = present.
imbr. = imbricate.
cont. = contorted.
exal. = not winged.
wing. = winged.
sup. = superior.
inf. = inferior.
div. = divided or fimbriate.

Coptosapelta off as a separate tribe placed near to the *Ixoreae*. Previously they had been considered as typical members of the *Cinchoneae*. He also suggested that certain tribes possessing similar pollination mechanisms, whereby the anthers are in close contact with the style which later carries the pollen upwards, should be associated together. This group contains the *Ixoreae, Gardenieae, Alberteae,* and *Vanguerieae* after certain anomalous genera have been removed from some of the tribes. The *Naucleeae* perhaps should also be included in this circle of affinity. In a further paper dealing with the *Rubiaceae* of Surinam (1934), he suggested the erection of several new tribes : *Sipaneae* for *Sipanea* and *Limnosipanea* (formerly *Rondeletieae*); *Manettieae* for *Manettia* (formerly *Cinchoneae*); and *Sabiceeae, Schradereae,* and *Coccocypseleae* for *Sabicea, Schradera,* and *Coccocypselum* respectively (formerly *Mussaendeae*). He associates the *Manettieae, Chimarrheae* (evidently another new tribe), *Cinchoneae,* and *Naucleeae* together, and also the *Morindeae, Coussareeae,* and *Psychotrieae*. In later papers some of these new tribes are not kept up. Bremekamp (1940) suggested that the fruit distinction between the *Hedyotideae* and the *Mussaendeae* was artificial and that the two tribes should be merged. He later entirely modified this view (vide infra). R. Utzschneider (1947) is one of several authors concerned with the derivation of the *Rubiaceae* as a whole. She denies that they are derived from either the *Umbelliferae* or the *Cornaceae* as had been suggested by Wettstein, Pulle and others and also indicated in the well-known family trees of Bessey and Hutchinson. She claims that the *Cinchonoideae* (in the old sense i.e. the subfamily containing the *Cinchoneae* and other tribes with locules with numerous ovules) are derived from the *Loganiaceae,* and that the *Coffeoideae* (the subfamily containing those tribes with uniovulate locules) were derived from the *Cinchonoideae* by reduction. Several genera fluctuated from one family to the other during this evolution and it is widely recognised there are still some genera (e.g. *Gaertnera*) the position of which is rather a matter of opinion. She thus seems to uphold the ovule character for the division of the *Rubiaceae* into two distinct compartments. If her ideas are correct it means at least that the many-ovuled ovary is primitive in the family but one-ovuled loculi may have been derived at different dates and not necessarily belong to plants which are to be considered a water-tight subfamily because of that character. Verdcourt (1952) suggested that the predominantly herbaceous

tribes (e.g. *Hedyotideae* and *Spermacoceae*, etc.) were probably much more closely related than the existing classification admitted (see also Verdcourt, 1950). The relationships between the tribes of the *Rubiaceae* have recently been discussed at length by Bremekamp (1952) in the introduction to his paper on the genus *Oldenlandia* sens. lat. In this account most of the characters which older writers considered fundamental are discounted — number of ovules in the ovary, nature of the fruit, presence or absence of a wing round the seeds,etc. Other characters such as the presence or absence of raphides, shape of the pollen, structure of the testa, mode of attachment of the ovules to the ovary walls, etc., are considered to be of much more importance. The *Morindeae*, *Coussareeae*, *Psychotrieae*, *Paederieae*, *Anthospermeae* and *Spermacoceae* all possess raphides, solitary ovules and valvate aestivation of the corolla; he claims they are related and form part of a natural group « *Rubioideae* ». The *Knoxieae* differ only in their pendulous ovules and can be accommodated in the group. The *Rubieae* (= *Galieae*) although characterised by the well-known distinct foliar stipules in almost all its members is to be grouped with the *Spermacoceae* since both tribes have pluricolpate pollen. The *Hedyotideae*, although they possess numerous ovules also have raphides in their tissues and a valvate aestivation; they too may be included in the subfamily *Rubioideae*. Raphides also exist in certain genera at present placed in other tribes : *Bouvardia*, *Heterophyllaea*, *Hindsia*, *Hymenopogon*, *Manettia*, *Danais*, *Coursiana* and *Hillia* were previously all considered to be members of the *Cinchoneae* on account of their winged seeds; *Deppea*, *Schradera*, *Lucinaea*, *Mycetia*, *Myrioneurum*, *Coccocypselum* and *Hamelia* formerly distributed in the *Rondeletieae*, *Mussaendeae* and *Hamelieae*. Most of these genera can be accommodated in the *Hedyotideae* but *Schradera* and *Coccocypselum* need new tribes. Raphides have been reported from certain other genera by Solereder and other anatomists but apparently in error. Bremekamp claims that the testa of the *Mussaendeae* s.s., *Rondeletieae*, *Condamineeae* and the *Cinchoneae* is of a similar structure and that these four tribes should be associated as a subfamily *Cinchonoideae*. He removes two groups of genera from the *Mussaendeae* on testa characters — the *Urophylleae* (21 genera allied to *Urophyllum*, *Pauridiantha*, etc.) and the *Pomazoteae* (10 genera). From the *Rondeletieae* several genera are excluded including *Gleasonia*. This genus he places in the *Henriquezieae* which tribe he considers

should be elevated to family rank and placed amongst the personate-flowered families near the *Bignoniaceae*. K. Schumann suggested that there were similarities between the *Henriquezieae* and the *Bignoniaceae*. For the group of tribes possessing the pollination mechanism previously discussed by Bremekamp in his earlier paper he suggests the subfamily name *Ixoroideae*. In this later paper a slight modification was made — the *Alberteae* s.s. do not have the same kind of pollination mechanism and are to be excluded from the *Ixoroideae* but certain genera formerly included in the *Alberteae* do have the mechanism and are not excluded. These genera form the *Cremasporeae*. The *Guettardeae* are distinct enough to need a separate subfamily of their own. In his 1952 paper Bremekamp considerably alters the composition of the tribe *Hedyotideae* (with which his paper is mainly concerned.) *Argostemma* is referred to a tribe of its own because of its united anthers which open by apical pores. It should be noted that this is not strictly true, since two species are said to have the anthers opening by slits (Ridley, 1927). Some genera are referred to the *Hedyotideae* from other tribes and others are excluded. *Pomazota* and its allies are referred to the *Pomazoteae, Spiradiclis, Ophiorrhiza* and *Virectaria* to the *Ophiorrhizeae,* and *Carlemannia* and *Sylvianthus,* two aberrant genera with dentate leaves and only two stamens to the family *Caprifoliaceae*. The transference of these two genera was first suggested by Solereder because of the fact that both exhibit peltate hairs rather like those of *Viburnum*. The majority of the facts do not support this conclusion. Bremekamp has not employed any of these new ideas to reclassify the *Rubiaceae* as a whole owing to the fact that insufficient information is available about many genera. He has divided the family into four subfamilies but indicated no relationship between them : *Rubioideae, Cinchonoideae, Ixoroideae,* and *Guettardoideae*. Several tribes are not placed and numerous genera excluded from tribes have no alternative affinity suggested.

II. — Criticism of the classifications proposed by previous authors.

The early classifications all share the fault that too few facts were used in their composition. They were very artificial with regard to their major divisions.

De Candolle's classification is straightforward. He appears to have employed the ovule character purely as a convenient means of dividing 13 tribes into two groups. He did not call these groups subfamilies nor did he give them names, but whatever significance he attached to the character it dominated the classification of the family during the next hundred years.

Bentham and Hooker's classification is essentially similar, the only difference being that they employ the same character to divide the tribes into three groups instead of two. Evolutionary ideas were just appearing at that date but they did not use them. Sonder in his treatment of the *Knoxieae* showed that he thought the ovule character alone was insufficient and in this one instance that habit was more valuable. Baillon's scheme is difficult to follow. He brings together very many morphologically dissimilar groups and the result is not only unnatural but impracticable.

K. Schumann's classification is overidealised and although based on previous artificial ones is made to appear as though it was « cut and dried » and based on entirely reliable characters. The family is divided into two subfamilies *Cinchonoideae* and *Coffeoideae* based entirely on the number of ovules. One would naturally infer that these groups were quite separate. He then proceeds to group tribes together in named « supertribes ». For instance the first division of his *Coffeoideae* is *Guettardinae* containing the *Alberteae, Knoxieae, Vanguerieae, Guettardeae* and *Chiococceae* i.e. the first half of Bentham and Hooker's series C. The only thing in common other than family characteristics is the position of the ovules in the loculi. Some of these tribes have more characters in common with tribes which appear in other supertribes than they have with each other. This state of affairs is unavoidable where a certain character A is used to divide a group and all the plants with that character negative are assumed to be related i.e. when the classification is based on a very small amount of the available evidence. This type of classification is in an arbitrary sense more definite than one based on numerous pieces of evidence of unequal value but is not a good classification. It is merely an artificial division of no use save for identification and even then it breaks down as more species are discovered. The reason such classifications are used is probably that once a single character is found which varies considerably and conveniently it provides a rapid method. Schumann had over 400 genera to arrange in a short

time and it was the presentation of a review of all the genera which really interested him and not their interrelations.

Hutchinson and Dalziel do not employ any new characters in their key to the *Rubiaceae* in the Flora of West Tropical Africa but differ from other writers in the relative importance to be assigned to the aestivation and ovule characters. It is not clear whether this is an artificial arrangement or the expression of the authors' ideas on a better classification of the family as a whole. It is presumed that the changes were made because it was realised that the older systems separated genera which are very similar. This shift of the emphasis to be accorded to the characters certainly brings some similar genera together which were formerly separated but in some instances it results in the converse.

No modern classification has been presented but it may be said that one is crystallizing slowly. Bremekamp has refuted the usefulness at tribal levels of nearly all the previously used characters and attempted to introduce a new set of characters which will obviate all the anomalies which had been accepted together with the old systems. For instance the genera *Tarenna* and *Pavetta* have always been recognised (even by Bentham and Hooker) as being so similar that the ovule character which separated them into different tribes must be considered unsatisfactory. There is no doubt that Bremekamp is correct in searching for new characters altogether and he has presented these in the introductory parts of the various monographs but has not yet attempted a complete reclassification of the family. Insufficient detailed work on all the genera has been done to do that. The actual criteria he uses are discussed in a later section.

Criticism has been made here of previous classifications of the family and it would be as well to discuss what a good classification is. It should be a convenient arrangement of the organisms concerned so that the species may readily be identified. It should be natural and bring together what appear to be related groups. Artificial classifications which for instance separate species on leaf shape tell one nothing else. Men could be divided into groups characterised by such pairs of characters as « blue eyes and long legs » but this would be of no value since the characters concerned have a random distribution throughout the species. When a classification is natural it is found that it is of value in many spheres; it has useful information locked up in it not apparent at first sight. Chemists are likely to find that genera or species grouped together

contain related compounds; entomologists may find that the insect they are investigating feeds on genera which are grouped together. In other words facts other than morphological ones confirm the classification. It is unlikely that special classifications i.e. those based on the presence or absence of a single character (e.g. presence or absence of raphides) or on the modifications of one type of character (e.g. chromosome numbers) will be good classifications. The ideal or « omega » taxonomy will produce classifications which will take into account the maximum number of characters including many which are not utilised at present (cf. Turrill, 1952). The relation between phylogeny and taxonomy is very well reviewed by Turrill (1942). Many classifications are based on apparent phylogeny e.g. Hutchinson's scheme for flowering plants. This is merely based on the assumption that certain characters are primitive. Probably the improvements this scheme sometimes has over others are due only to the consideration of new facts. Phylogeny or at least the evolutionary concept is bound to have some effect on taxonomy e.g. in major classifications of Kingdoms simple organisms will be placed first. It is widely recognised however, that ideas on phylogeny are not compatible with practical classifications. This has been found to be true for molluscan groups where the fossil evidence is very well documented indeed. It has, moreover, been pointed out by Hayata (see Airy Shaw, 1950) that morphological characters do not necessarily denote phylogenetic relations and hints that phylogeny is illusory. Rather he finds infinite relations (sic) between large numbers of groups not usually associated by any of the accepted schemes. There may be in fact an infinite reticulation of characters. The more characters which are considered, the more difficult it is to place a group in any given scheme and, moreover, its position will vary according to the actual characters considered. For instance some « distant » groups share characters with the *Rubiaceae*. Airy Shaw *(in litt.)* suggests that the *Naucleeae* show links with the *Combretaceae*, some *Rubieae* and *Hedyotideae* show Gentianaceous tendencies; *Carlemannia* and *Silvianthus* have Acanthaceous links; *Mussaenda* and *Warszewiczia* Hydrangeaceous and *Ixora* Verbenaceous. These heterodox views indicate how valid phylogenetic data (when available) are likely to affect classifications of the family. It is best that putative evolutionary relations should not come into the making of a practical classification. This applies more particularly to larger groupings.

III. — The available criteria and their discussion.

A) *List of the characters.*

The characters are listed below. Certain such as venation and texture of the leaves, arrangement of the subsidiary cells of the stomata, flower colour, and anther shape have been examined and found of no value above specific level since they do not correlate with other criteria found to be reliable.

1. Habit and growth forms.
2. Stipules.
3. External indumentum.
4. Inflorescence.
5. Flowers : shape; aestivation; presence of unequal calyx lobes; corolla throat hairs; stigma shape; ovules and placentae; pollen; heterostyly and unisexuality; pollination mechanisms.
6. Fruit and seeds : nature and dehiscence of fruit; presence or absence of a wing around the seeds; structure of testa cells; presence of albumen.
7. Anatomical data.
8. Cytological data.
9. Physiological and biochemical data; aluminium accumulation; presence of raphides.
10. Distribution data.
11. Links of affinity between members of different tribes.

B) *Discussion of the characters.*

1. Habit is a character which is of most value at generic levels but the distribution of growth forms in the family indicates definite tendencies. All the predominantly herbaceous tribes are contained in the group Bremekamp has termed the *Rubioideae* i.e. it partly correlates with the presence of raphides. This subfamily is not however entirely herbaceous and contains several woody tribes. The other subfamilies are almost entirely composed of trees and shrubs with a very few herbaceous members perhaps derived from the woody members. It is well-known that very many woody genera e.g. *Combretum* contain a very few herbaceous species or diminutive subshrubs (usually pyrophytes). The genera *Fadogia*

and *Pygmaeothamnus* are pyrophytic subshrubs in the predominantly woody tribe *Vanguerieae*.

2. Stipules vary in the *Rubiaceae* from simple to multifimbriate. The latter greatly predominate in the herbaceous tribes and some other *Rubioideae* but several other included genera have entire ones. Moreover, bifid or divided stipules appear in tribes excluded from that subfamily, but sufficiently rarely for the character to be a valuable preliminary pointer as to the position of a plant.

3. The external indumentum of many *Rubiaceae* belonging to all the tribes recognised by various authorities has been examined and the results may be found in the appendix (1). Hairs in the family are of three main types: septate, uniseriate, composed of separate cells; incompletely septate i.e. hairs with rather thick walls and the lumen with weak or strong septae which do not cut the walls; and non-septate hairs. Septate hairs on the leaves and outside of the flowers definitely occur only in the *Rubioideae* but many plants in that group are glabrous or have short unicellular hairs. Septate hairs certainly arose in the Angiosperms on several separate occasions in very diverse families. In the *Rubiaceae* however, it is possible that they have arisen on a single occasion. The genera in the *Rubioideae* not possessing septate hairs usually have thin-walled short papilla-type hairs which could have been formed by reduction. Various species in the genus *Pentas* confirm this possibility, hairs being found which are composed of 1-10 cells. Other subfamilies have hairs of varying kinds but I have not found any truly septate ones. Rather thick-walled round hairs are the general rule. Hair structure is therefore a useful secondary character but too subject to exceptions for use as a major criterion.

4. The type of inflorescence is usually constant for a given genus e.g. in *Pentas* it is a terminal complicatedly branched cymose arrangement and in *Otomeria* it is a very reduced cyme resembling a spike; but it varies in some tribes or groups of genera. The aggregate of genera formerly included in *Oldenlandia*, but now segregated, contain species with axillary or terminal inflorescences. There is no doubt that these genera are morphologically so similar that their generic distinctness is open to severe doubt. The position of the inflorescence is of little more than generic significance in most cases. The structure of the inflorescence is important in some tribes e.g. *Naucleeae* and *Schradereae* which have a compact and

usually spherical inflorescence. Similar types occur in *Bertiera* and *Morinda*.

5. The shape of the corolla varies from infundibular, tubular, to rotate in various members of the family. The hypocrateriform type may be discovered in almost every tribe. As a character it is scarcely of generic value. In the genus *Gardenia* as at present constituted and admittedly artificial it is only specific. Aestivation has been used by Hutchinson as a major character. It would be easy to dismiss it, however, as being without value since in a tribe the members of which appear to be genetically related on the available evidence e.g. the *Naucleeae*, both imbricate and valvate aestivations occur. In the *Cinchoneae* all three types occur even when certain aberrant genera are removed to other tribes. In one subfamily the character has more value and I see no reason why a character should not have unequal value in different groups of the same family. The subfamily *Rubioideae* with very few exceptions contains only species with valvate aestivation.

A very characteristic feature of the family is the continual recurrence of genera with unequal calyx lobes, one or more being enlarged, often considerably so. The following tribes contain such genera :

Condamineeae (*Pinckneya*, etc.; much enlarged); *Hedyotideae* (*Pentas, Otomeria*, etc.; usually little enlarged); *Rondeletieae* (*Warszewiczia*, etc.; much enlarged); *Cinchoneae* (*Calycophyllum;* much enlarged); *Mussaendeae* (*Mussaenda, Pseudomussaenda;* much enlarged); *Alberteae* (*Nematostylis;* little enlarged); *Knoxieae* (*Pentanisia*, etc.; little enlarged); *Psychotrieae* (*Declieuxia* etc.; little enlarged); *Anthospermeae* (*Otiophora;* little enlarged).

The occurrence of this character is so sporadic that its only practical importance is in identifying those species and genera which show it. Certain tendencies are again noticeable however, which may be significant. Very enlarged coloured sepals are a feature of those tribes associated with the *Cinchoneae* whereas slightly enlarged greenish sepals occur in the *Rubioideae*. Their occurrence is not even constant in one genus however e.g. in *Mussaenda* and *Pentas* some species have unequal lobes and others have equal ones. The large white bracts in some *Faramea* spp. and *Morinda* spp. are true bracts and not connected with the calyx.

Hairs occur in the inside of the corolla in numerous genera and species of the family. The occurrence is not constant even within a single apparently natural genus (e.g. *Otiophora*). Very many of these hairs have been examined in representative species from

all the tribes (see appendix 1). In all the species examined, save two, the hairs are non-septate and usually flat and ribbon-like. This is probably a feature of many families, certainly of the *Loganiaceae*. The two exceptions are *Otiophora pycnostachys* K. SCHUM. and the genus *Timonius*. In the *Otiophora* the hairs are prominently septate, in the *Timonius* feebly and incompletely so, and in both cases the hairs are on the filaments and not the style or throat proper. For some reason these hairs are homologous with the external type of indumentum rather than the internal found in many other genera (actually absent in both cases). The shape and ornamentation of the internal hairs is very diverse — some are very closely striate (e.g. *Pentas, Mussaenda*); others warted — some have straight walls and others such as the cushion-type Socotran species of *Oldenlandia* are so constricted that very careful examination is necessary to see that the hairs are non-septate. The same type of ornamentation occurs in different tribes but it is a character which could be made more use of at specific levels.

In the *Compositae*, a family placed near to the *Rubiaceae* by all the classifiers of the Dicotyledons, the nature of the style is considered to be of paramount importance. The style in the *Rubiaceae* may be clavate, 1-∞-fid, or capitate and the stigmatic processes variously placed. In the *Vanguerieae* the capitate style is one of the most characteristic features and it will be shown (page 240) that some genera referred to that tribe but with another type of style have been wrongly placed. The *Rubioideae* usually have the style divided into linear lobes with stigmatic papillae both on the insides and outsides of the lobes. Other tribes have both clavate and divided styles. In those tribes with the « ixoroid » pollination mechanism (see below) the stigmatic surfaces are at first hidden.

As has already been mentioned the ovule character has been the one assigned most importance by the early writers. It was realised to a certain extent that genera which are almost certainly genuinely related and even species of one genus were forced into different subfamilies. Certain exceptions had to be allowed — a very few species in the *Hedyotideae* notably in such genera as *Anotis* have very few or solitary ovules whereas the rest of the tribe have numerous ovules. The *Naucleeae* are characterised by numerous ovules but *Cephalanthus* has solitary ovules. The identity of the genera *Kraussia* and *Rhabdostigma* formerly sepa-

rated by ovule characters is a further example of the character breaking down. All characters are subject to exceptions even the best, and this is not really of importance; in fact the ovule character could not be attacked merely on the basis of exceptions since characters which are accepted as of major value in other families are subject to many more exceptions. What is considered important is that the purely arbitrary difference between '1' and 'greater than 1' is used to divide the family into two supposedly widely divergent groups. This results in two species such as *Borreria ocimoides* and *Oldenlandia verticillata* being placed as far apart as they could possibly be, whereas in general morphology they are similar. Such a classification indicates in fact that the *Borreria* is more closely allied to a *Vangueria* for example than it is to the *Oldenlandia*. A glance is enough to show that this is very unsatisfactory. The ovule character is most useful at tribal and generic levels but varies in a given subfamily and even in a tribe. It is plausible that ovule-number is a character which could vary very rapidly in a relatively short time. The nature of the placenta is also valuable and its position in the loculus. The number of locules in the ovary is of little value. Amongst the *Knoxieae*, *Calanda* (= *Otocephalus*) has a 1-locular ovary and in one inflorescence of *Pentanisia ouranogyne* Sp. Moore 2-, 3-, 4-, & 5-locular ovaries can be found side by side. The *Coussareae* are 1-locular in fruit.

The pollen grains of the *Rubiaceae* have been discussed to a certain extent by Bremekamp (1952) and by Erdtman (1952). Judging by his figures it appears that the first author did not examine acetolysed material. Neither author appears to have described pollen from every tribe. I have prepared acetolysed pollen from at least a few members of each tribe and the results are given in the appendix and plates. Wodehouse states that pollen grains although of very great value at specific and generic levels, must be used cautiously for making generalisations. Related species (sic) have similar grains if the internal and external environments are the same but pollen grains of truly related species have diverse grains if this condition does not apply. The meaning of internal environment in this context is not evident. The types of grain occurring in the *Rubiaceae* may be classified as follows :

1. Specialised types.
   a. Cylindrical grains with two very large pores — some *Coussareeae*, others including most *Faramea* are 3-porate. According to Erdtman these grains

exhibit a marked similarity to certain cretaceous sporomorphs but it is dubious if any significance is to be attached to this.

b. Tetrahedral tetrads of 3-porate grains with little or no sculpture, restricted to the *Gardenieae* proper but not occurring in any but a small percentage of that tribe. Not all the species of the genus *Gardenia* itself have tetrads but it must be remembered that the genera *Randia* and *Gardenia* need reclassifying. Keay (1958) (3) published a valuable paper on this group. The pollen character was of great assistance.

2. Porate grains. 3-4 porate. These occur in the *Cinchoneae* (*Coptosapelta*, placed in a separate tribe by Bremekamp), *Condamineeae (Bikkia)*, *Mussaendeae*, *Hamelieae (Hamelia)*, *Gardenieae*, *Ixoreae (Morelia)*, *Guettardeae* (all species examined), *Vanguerieae* (all species), *Morindeae*, and *Psychotrieae*. The porate grains of the *Coussareeae* are unique in certain respects (Erdtman, 1952).

3. Colpate grains. 3-4(-5)-colpate. These are the usual type found in the family and occur in all tribes except the *Vanguerieae*, *Guettardeae*, *Coussareeae*, *Spermacoceae* and *Rubieae*. The shape and ornamentation often varies within the genus. To illustrate the variation of grains in one genus several species of *Pentas* are figured in the plates.

4. Pluricolpate grains 5-25-colpate. These are characteristic of the *Spermacoceae* and *Rubieae*. Two kinds may be distinguished :

   a. Disc-shaped grains usually large with short and numerous colpi on the rims only (confined to the *Spermacoceae*).

   b. Ellipsoidal grains with fewer longer colpi extending over the body. Grains smaller (occur in both tribes).

Pollen grain characters are therefore not suitable as the main character for subdividing the family. Similar grains occur in diverse tribes and subfamilies. The tribes mentioned in the fourth group are well-characterised by their pollen. Many genera are similarly characterised (e.g. *Virectaria*). A very much wider survey of genera is needed than was possible with the material available.

Unisexual flowers occur in the *Anthospermeae* and in a few of the very dissimilar *Gardenieae*. Some *Rubieae* (e.g. Australian species of *Asperula*) are also unisexual. In the *Anthospermeae* unisexuality may be extreme evolution from heterostylous forms. *Anthospermum herbaceum* L. F. is heterostylous but often one finds a pronounced female plant with enormous styles and obsolete anthers. Certain genera which are included in the *Anthospermeae* are hermaphrodite.

Heterostyly is a very prominent feature in the *Rubiaceae* and occurs in numerous genera, although it was at first overlooked and noticed in very few (e.g. *Otomeria*, Hiern, 1877). In some genera it has been so overlooked that species have been distinguished on whether or not the anthers were exserted (vide Brenan, 1949 and Bremekamp in Pulle, 1934). It could never be a major character since even in one genus some species exhibit heterostyly and others

(3) Published after this paper went to press.

do not e.g. *Otomeria* and *Pentas*. In *Pentodon pentander* there are even varieties which do or do not exhibit heterostyly. Nevertheless it is interesting to see just which genera do show it. A rapid survey of all the genera available at Kew indicated that most of the plants showing it are herbaceous and it is rarer in arborescent species. It is undoubtedly commonest in those tribes referred to the *Rubioideae* being very frequently shown by members of the *Morindeae, Hedyotideae, Cruckshanksieae, Knoxieae, Psychotrieae, Paederieae, Spermacoceae,* and *Anthospermeae*. Certain members of the *Mussaendeae, Urophylleae, « Hamelieae » (Heinsia),* and *Rondeletieae (Sipanea)* also show it but not all of these show what may be called complete heterostyly i.e. style exserted and anthers completely included in one form and exactly vice versa in the other. Even in the *Hedyotideae* (e.g. *Pentas* subgenus *Megapentas*) some species have the anthers constantly included but the style of varying lengths in different forms. *Pseudomussaenda* and *Heinsia* exhibit this kind of heterostyly and some species of *Sipanea* have the anthers at different heights in the corolla tube. From herbarium studies I at first thought that *Guettarda* exhibited incomplete heterostyly but a study of the living plant at Mombasa shows that the style elongates after the flower opens. Apart from these, certain genera formerly included in the *Cinchoneae* and *Vanguerieae e.g. Danais, Schismatoclada,* and *Craterispermum* also show complete heterostyly. It is demonstrated on pages 240 and 244 that these genera have been quite wrongly placed in the past. Some other genera appear heterostylous from herbarium material e.g. *Lagynias* but this is illusory and due to the fact that the slender style readily breaks. Complete heterostyly occurs only in the *Rubioideae* but is a character of limited value. It may have arisen on numerous occasions independently which destroys the value of any character. For example slugs are defined as molluscs that have no external shells but internal anatomy indicates that the shell was lost on three separate occasions and that the three groups are not related. This kind of convergence can be misleading.

The heterostyly mentioned above is presumably connected with pollination but a close study of *Pentas lanceolata* (Forsk.) Deflers has not shown any obvious mechanisms to ensure cross-pollination such as occur in *Primula*. Bremekamp has used the mechanism exhibited by e.g. *Pavetta* to characterise a group of tribes *(Ixoroideae)*. It is difficult to assess the value of this character purely

by herbarium studies, and very much more field work needs to be done. I have observed the mechanism in several species of *Pavetta;* in *P. elliotii* K. SCHUM. observed near Nairobi (see Pl. XVI f. K) the clavate style is touching the introrse anthers in the unopened bud. Seven longitudinal lines of short hairs on the style fit in the grooves of the closely touching anthers, and slightly prolonged connectives fit over the apex of the style. When the bud opens the pollen is already adhering to the stigma and the anthers are empty. The style then grows rapidly upwards until well-exserted. The stigmatic surfaces at the apex of the style, which is slightly excised, open outwards. There is abundant nectar at the base of the corolla tube and this particular species is pollinated by the Silver-striped Hawkmoth. A similar mechanism undoubtedly occurs in the *Vanguerieae*. The character has a practical disadvantage; only in fresh herbarium specimens does the pollen still adhere to the style. The mechanism entails by its very nature that in the mature bud the style is in contact with the introrse anthers whereas very shortly afterwards it is well exserted. This is not difficult to observe in an inflorescence containing both buds and opened flowers. In other groups the style does not grow in this way e.g. in a macrostylous *Pentas* the style is well exserted from the tube in bud. The style need not necessarily be clavate in the genera showing the ixoroid mechanism, but if divided then the lobes are joined together until the style has been exserted — e.g. *Coffea* has long linear lobes. The stigmatic surfaces are not exposed until the lobes divide. The use of this character to characterise a subfamily as done by Bremekamp introduces difficulties. Certain genera in the *Cinchoneae* possess the mechanism. Bremekamp removes two, *Coptosapelta* and *Crossopteryx* to a separate tribe. *Hymenodictyon* would have to be added and probably *Corynanthe* also. Of these four genera only the first is otherwise out of place in the *Cinchoneae*. The *Naucleeae* possess the mechanism but also closely resemble the *Cinchoneae*. Bremekamp claims that even those species of the *Gardenieae* which are unisexual have the mechanism because the style is well-developed in the male flowers.

6. The nature of the fruit, whether succulent or dry, figured quite largely in the older classifications in order to distinguish tribes. This distinction is insufficient and its value may be estimated from the fact that in the genus *Pentanisia* which I believe to contain

species all derived from the same ancestor, some have dry indehiscent fruits, some have dicoccous fruits with the cocci indehiscent and some have succulent ones containing pyrenes. *Pseudomussaenda* differs very little from *Mussaenda* save that the former genus has a capsular fruit and the latter more or less succulent indehiscent fruits. The nature of the dehiscence is of more importance than the hardness or softness of the pericarp. The following types of fruit occur in the family :

Dehiscent :

loculicidal or septicidal capsules without beaks (e.g. *Pseudomussaenda*);
loculicidal or septicidal capsules with beaks (e.g. *Pentas*).

Indehiscent :

dry fruits separating into two cocci or pyrenes (e.g. *Pentanisia prunelloides*);
dry fruits which are quite indehiscent (e.g. *P. ouranogyne*);
succulent fruits containing pyrenes (e.g. *Psychotria*);
succulent fruits with uncovered seeds, drupes and berries (e.g. *Pavetta, Mussaenda*);
succulent fruits aggregated in syncarpia (e.g. *Nauclea* and *Morinda*);
fruits with leathery pericarps and seeds embedded in a gelatinous mass (e.g. *Randia*).

The nature of the fruit is not a valuable character for defining major groups within the family. The *Ixoreae* group of tribes have mainly succulent fruits and the *Cinchoneae* group dry fruits. The *Guettardoideae* have characteristic drupes. The *Rubioideae* display a wide range of types. There are numerous exceptions and the character is one of the most misleading of all.

The presence or absence of a wing around the seeds has been considered of importance but Bremekamp refutes this. Notwithstanding, it is true to say that many of the *Cinchoneae* and associated tribes have winged seeds. Several genera referable to the *Hedyotideae* (including *Danais* once put in the *Cinchoneae*) have winged seeds. The character is of no use above tribal rank but I do not agree with Bremekamp that it has no value at all.

Bremekamp has emphasised the importance of the structure of the testa and I have examined this character for numerous species. The presence of large pits in the bottoms of the cells in members of the *Cinchoneae* group of tribes is a character which is readily seen, but other characters which he employs are very difficult to see and certainly not suitable for practical use. Some such as the presence of oil drops and wavyness or straightness of the walls may even vary with the method of preparation of the material

under investigation. Corner (1941) has some caustic comments about minute characters used by Bremekamp to separate Malayan *Ixora* species, but they are really directed against splitting and I am in equally strong disagreement with this. Corner himself advocates that more use should be made of such neglected characters as scent and gloss. The results of my investigations into the testa character have convinced me that it is not such a sound character as Bremekamp implies. Without a much more detailed classification of the types of testa, the mere use of the word pits is insufficient. Pits or thinnings of various kinds have been found in several tribes e. g. *Naucleeae, Cinchoneae, Condamineeae, Rondeletieae, Mussaendeae, Gardenieae, Guettardeae, Chiococceae, Vanguerieae* and *Morindeae*. Bremekamp would doubtless reply that these pits had different structures and this is to a large extent true. Actually the pits are not always clearly pits but the lumen sculpture would be better described as a reticulation of anastomosing ribs. In his 1952 paper he states that the genus *Gleasonia* is to be removed from the *Mussaendeae* and placed in the new family to be formed from the *Henriquezieae* because of the exalbuminous seeds and the very peculiar structure of the testa. If his figure of the two testae is examined (Tab. 5 c and e) it will be seen that they differ from each other quite as much as any other pair of testae figured. Similarly the genus *Manostachya* (a dubious generic split from *Oldenlandia*) is very distinctly shown as having a pitted testa (tab. 8, fig. a) quite as pitted as that of *Gonzalagunia* (tab. 3, fig. d) and yet the first genus belongs to the *Hedyotideae* and the second to the *Mussaendeae* and to two different subfamilies supposed to be distinguished by the testa. In the text no mention is made of the presence of pits in the genus *Manostachya* but the structure is called a network of ridges, which as I have stated, better describes some of the other pitted testae. Pits are scarcely visible in *Condaminea corymbosa* one of the *Cinchonoideae*. The *Ixora* group of tribes are referred to a separate subfamily on account of their pollen mechanism, but the *Naucleeae* which also show it are said to be better placed in the *Cinchonoideae* because of their pitted testae. A group of genera usually placed in the *Cinchoneae (Coptosapelta, Crossopteryx* and *Hymenodictyon)* all show the ixoroid pollen mechanism or appear to but the latter pair have distinct pits in the testa cells. In this case Bremekamp removes these genera from the *Cinchoneae* to a new tribe in the *Ixoroideae*. He also suggests as a partial way out

of the difficulty that the *Naucleeae* are «perhaps no natural group». I consider them to be one of the most natural groups in the family and most botanists think similarly (Hiern, Bentham and Hooker, Airy Shaw, Haviland). There is a good deal to be said for judging a group to be natural by the « look of it » however unscientific this may sound. An experienced taxonomist takes into account subconsciously an infinite number of subtle characters and there is nothing to be gained by splitting up a group which gives every appearance of being natural and is readily identifiable, without very strong evidence indeed. It certainly should not be done as a way out when one's characters do not behave as one wishes them to ! Bremekamp further states that the presence of pits in the testa cells never coincides with the presence of raphides. Apart from *Manostachya,* material of which has not been examined, the genus *Deppea* definitely contradicts this statement. Fruiting material was not available to Bremekamp but I have seen several species in fruit. The capsules are usually decidedly like those of the *Hedyotideae*. I have examined the testa of *D. cornifolia* and pits are definitely present. Raphides are not abundant in the leaf tissues but are more frequent in the corolla lobes. With regard to all these criticisms it must be remembered that all the characters in use at the present time have many exceptions. The rejection of a character because certain exceptions occur would mean the rejection of a very large number of the criteria used in all groups of both animals and plants. The test must be whether or not the use of the character confirms the classification based on the characters which have been taken to be reliable.

Albumen is only absent in the *Guettardeae* and « *Henriquezieae* » and since the *Guettardeae* are in many ways aberrant the absence of albumen is a good technical character helping to separate them, though difficult to use in practice.

The position of the radicle has been used by Bentham and Hooker as a tribal criterion. It is linked up with the position of the ovules, a character already discussed. It is a difficult character to use. The radicle is predominantly inferior in the *Rubioideae* but is superior in the *Knoxieae* and *Craterispermum*. These are the only two components of the *Rubioideae* with solitary descending ovules, which reverses the position of the radicle with respect to the hilum. In the *Hedyotideae* where there are numerous ovules variously orientated the position of the radicle is meaningless.

7. The anatomy of the *Rubiaceae* is discussed by Solereder and Metcalfe and Chalk in their well-known textbooks. I have thoroughly examined this mass of detailed information but could find nothing which was useful to me as a primary dividing character. Anatomy is certainly of value in helping to solve the position of anomalous genera e.g. *Gaertnera* is Rubiaceous rather than Loganiaceous. One tribe, the *Rubieae,* does have a constant anatomical character running through it which is undoubtedly of value — all have polygonal stems with collenchymatous ribs.

8. Although a considerable number of plants belonging to the family have been subjected to chromosome counts very little work has been done from the taxonomic point of view. Sufficient has been carried out, however, to show that a complete cytological investigation of the entire family would be of very little assistance in classification at tribal level. Turrill (1942) states that very little cytogenetical work has been of value above the specific level. Darlington and Janaki Ammal (1945) summarise results from seven sources and it appears that x = 9, 10, 11, 12, 14 or rarely 17 with 2-12-ploidy. X = 11 predominates and occurs in diverse tribes. The question naturally arises whether the tribes are natural or whether the data are confused because they are artificial. If all the genera with for instance x = 10 are considered as a group it is found to be entirely heterogeneous with regard to all the other characters. The tribe *Rubieae* is apparently most natural but it has the most varied chromosome numbers and, significantly, has been more subject to investigation than any other tribe. The available data are summarised below :

Rubieae	x = 9, 10, 11 or 12 with 2-12-ploidy.
Hedyotideae	x = 9 or 10 with 2-8-ploidy.
Rondeletieae	x = 10 or 11 with 4-ploidy.
Naucleeae	x = 11 with 4-ploidy.
Psychotrieae	x = 11 with 2-4-ploidy.
Paederieae	x = 11 with 4-6-ploidy.
Anthospermeae	x = 11 with 2-4-ploidy.
Vanguerieae	x = 11 with 4-ploidy.
Spermacoceae	x = 14 with 2-ploidy.
Condamineeae	x = 11 with 2-ploidy.
Coptosapelta	x = 11 with 2-ploidy.
Mussaendeae	x = 11 with 2-?-ploidy.
Cinchoneae	x = 10 or 11 with 2-4-ploidy.
Ixoreae	x = 11 with 2-8-ploidy.
Gardenieae	x = 11 with 2-ploidy.
Catesbaeeae	x = 12 with 2-ploidy.
Hamelia	x = 12 with 2-ploidy.
Hoffmannia	x = 12 with 4-ploidy.
Posoqueria	x = 17 with 2-ploidy.

Bouvardia and *Manettia* both have x = 9 which agrees with their transference from the *Cinchoneae* to the *Hedyotideae*. The *Spermacoceae* appear to be isolated on this preliminary evidence and *Posoqueria* has been excluded from the *Gardenieae* on other grounds by Bremekamp.

9. The family *Rubiaceae* provides several alkaloids. *Cinchona* is renowned as the source of quinine. Others are obtained from *Mitragyna (Naucleeae), Corynanthe (Cinchoneae), Psychotria* and *Cephaelis (Psychotrieae),* etc. The *Cinchona* group of alkaloids are derived from quinoline whereas the *Psychotria* group are derived from isoquinoline. Far too little is known about the structure of the alkaloids for them to give any help with the classification.

Certain members of the *Rubioideae* contain foetid substances which may or may not be of related structures. They do not appear to have been investigated but may be isothiocyanates. They occur in *Coprosma* spp. *(Anthospermeae), Pentanisia foetida* Verdcourt *(Knoxieae)* and the *Paederieae* (most members).

The subject of comparative aluminium accumulation by various groups of plants has been investigated by Chenery (1948). His results are summarised here. He found that the family contained the largest number of accumulators of any which he studied — 647 species in 91 genera were accumulators. In the following list the data in brackets following the tribal name indicate the number of accumulators.

Naucleeae (none); *Cinchoneae* (very few); *Henriquezieae* (none); *Rondeletieae* (none save *Acrobotrys*); *Condamineeae* (none); *Hamelieae* (none); *Hedyotideae* (in only six genera); *Mussaendeae* (in sixteen genera); *Catesbaeeae* (none); *Gardenieae* (none save *Scyphostachys*); *Cruckshanksieae* (none); *Guettardeae* (none); *Retiniphylleae* (none); *Knoxieae* (in all save one genus); *Chiococceae* (none save *Asemnantha*); *Alberteae* (in three genera); *Vanguerieae* (in three genera and *Calanda* which is to be placed in the *Knoxieae*); *Ixoreae* (in a few species of *Pavetta*); *Morindeae* (in all save two genera); *Coussareeae* (in all); *Psychotrieae* (in most genera which are usually marked accumulators); *Paederieae* (none); *Anthospermeae* (in *Mitchella* and *Coprosma*); *Spermacoceae* (in four genera); *Rubieae* (*Galieae,* in a few species of *Rubia* and *Relbunium*).

It is not a character of very great value at higher levels since tribes and even genera can contain both accumulators and non-accumulators. It tends to confirm the association of the *Psychotrieae, Morindeae* and *Coussareae*. It is a useful character to confirm the removal of genera from one part of the classification to another. The association together of *Coptosapelta, Crossopteryx*

and *Hymenodictyon* is not supported since all the species of the first genus are accumulators but none of the species of the other two is. Most of the genera separated by Bremekamp from the *Mussaendeae* are accumulators whereas most of those left in it are not.

Bremekamp is responsible for the introduction of the study of certain calcium oxalate crystals as a possible character. The possession of these crystals by members of the family was well-known to Solereder and others. I consider this character a good one, when the particular type of crystals known as raphides are studied i.e. bundles of needle-shaped crystals usually enclosed in mucilage cells (Pl. VIII f. A & B) or rather thicker crystals not so enclosed. The group of tribes brought together when this character is considered of primary importance seem to have other reliable characters in common. One is impressed with this when one has worked with the family in the herbarium and had to name hundreds of its members over a period of years. I have examined some thousands of specimens of African and extra-African *Rubiaceae* belonging to all the tribes, in order to investigate the validity of this character. Their universal presence in the group of tribes forming the *Rubioideae* is unquestionable. Those genera which Solereder claims have raphides but which are not members of the *Rubioideae* (in my sense) do not actually possess them as Bremekamp points out e.g. *Coffea* and *Coptosapelta* have no raphides. These contradictions are probably due to a misunderstanding over crystal types e.g. small prismatic crystals occur in *Canthium crassum*. I disagree with Bremekamp over certain genera. They do occur in *Urophyllum*, *Pauridiantha*, *Ophiorrhiza*, and *Spiradiclis* and the position of these genera will be mentioned later. I am probably taking a rather wider view of raphides than Bremekamp has done by including thicker needle-shaped crystals not occurring in dense bundles. In *Deppea* the raphides are difficult to observe but I agree that they are present. *Ophiorrhiza succirubra* KING and *O. mungos* L. have been examined and bundles of raphides are definitely present, chiefly in the leaf vein tissues, but the crystals are admittedly very slow to separate out when the tissues are macerated in water. Similar bundles of crystals are even more abundant in the leaf tissue of *Spiradiclis caespitosa* BLUME. Metcalfe and Chalk also agree that raphides are present in these two genera. Bremekamp *(in litt.)* denied the presence of raphides in a specimen of *Tapinopentas ulugurica* VERDCOURT which was sent to him but I found

them to be very abundant. There is no reason why this crystal character should not be attributed real importance and why it should not form the basis of a classification. It is not an unsatisfactory character from a practical point of view since a rapid microscopical examination will quickly reveal the presence of raphides — they may often be seen merely by holding a leaf up to the light. Details of ovary structure used in the older keys are often more difficult to observe. Whilst searching for raphides I used polarised light; crystals of all kinds can then be picked out instantly, even in those genera where they are admittedly difficult to observe. When examining a plant the leaf, flower and fruit tissues should all be examined since there is often a marked concentration of raphides in these organs (e.g. fruits of *Lasianthus*).

The choice of hosts of various insects and fungi often points to affinities but few data are available. Coffee pests have other generations on *Pavetta* and *Psychotria* spp. Bacterial nodules occur in only three genera — *Pavetta, Grumilea,* and *Psychotria.*

10. Phytogeography sometimes gives help in the classification of groups of plants. The main facts concerning the distribution of the *Rubiaceae* are given below. The family is very widely distributed indeed, which indicates that it is probably a very ancient one :

Anthospermeae (worldwide including Australasia and Oceania); *Albertieae* (Africa); *Cinchoneae* (mostly Sth. American but also Africa, Asia, and Pacific excluding Australia); *Chiococceae* (Central and South America, Australia); *Condamineeae* (South and Central America, Malaysia; Wernham refers the African genus *Pseudomussaenda* to this tribe); *Coussareeae* (Central and South America, one genus *Schizocolea* BREM. in Africa) : *Gardenieae* (almost worldwide, not in New Zealand or Holarctic territories); *Guettardeae* (mostly South America but also African coast, Asia, Australia, Polynesia); *Hedyotideae* (worldwide but not in North Eurasia or New Zealand); *Ixoreae* (South America, Africa, Asia, Malaya and Australia); *Knoxieae* (Africa, India and Australia); *Mussaendeae* (South America, Asia, Malaya, Africa); *Morindeae* (worldwide but not in Eurasia or North America save Florida); *Naucleeae* (worldwide but not in Holarctic territories or New Zealand); *Psychotrieae* (as last); *Paederieae* (Africa, South and South-East Asia and South America); *Rondeletieae* (South and Central America, Malaysia and also recorded from the Near East); *Rubieae* (worldwide including Holarctic territories, New Zealand, etc.); *Spermacoceae* (worldwide excluding New Zealand); *Vanguerieae* (almost wholly African, a very few in Malaya).

Other tribes used by some authors are added below :

Argostemmateae (West Africa, India and Malaya); *Catesbaeeae* (South and Central America); *Coccocypseleae* (Brasil); *Coptosapelteae* (Africa and Malaya); *Cremasporeae* (Africa); *Hamelieae* (South and Central America, Africa); *Ophiorrhizeae* (Africa, Asia and Australia); *Perameae* (South America); *Poma-*

zoteae (East Asia); *Retiniphylleae* (South America); *Schradereae* (South America); *Urophylleae* (Africa, Asia, Malaya and Japan).

A list of the genera having a wide distribution is given below and is of some interest since the genera concerned may be among the oldest in the family.

Oldenlandia (worldwide even when restricted sensu Bremekamp); *Anotis* (Himalayas, Ceylon and Australia); *Pentodon* (one species in Florida and Africa); *Argostemma* (West Africa, Tropical Asia, Himalayas and Malaya); *Lindenia* (Central America and Fiji); *Hymenodictyon* (Asia and Africa); *Adina* (Asia, Africa and Japan); *Mitragyna* (Malaya and Africa); *Uncaria* (Africa, Asia, America and Australia); *Cephalanthus* (Africa, America and Asia); *Nauclea* (Africa, Asia and Australia); *Mussaenda* (Old World and Polynesia but not Australia); *Sabicea* (America, Africa and Madagascar); *Tarenna* (Asia, Africa and America); *Randia* aggreg. (worldwide in tropics); *Gardenia* (old world tropics); *Scyphiphora* (India and Australia); *Tricalysia* (Asia and Africa); *Knoxia* (Australia and India); *Bertiera* (America and Africa); *Guettarda* (America and one in the Old World); *Antirrhoea* (East Asia, Madagascar, Mauritius and Cuba); *Coffea* (Africa and Malaya); *Pavetta* (Africa, Asia and Australia); *Ixora* (America, Africa and Asia); *Mapouria* (America and Malaysia); *Psychotria* (pantropical); *Grumilea* (Asia and Africa); *Chasallia* (ditto); *Geophila* (Asia, Africa and Pacific); *Uragoga* (Asia, Africa and America); *Lasianthus* (Asia, Australia and Africa); *Paederia* (Asia, South America and Africa); *Nertera* (South America, Tristan, New Zealand, Sandwich and Malaya); *Coprosma* (Chili, New Zealand, Pacific, Australia, Malaya and Sandwich Islands); *Mitchella* (Japan and North America); *Morinda* (Africa, Antilles, Florida, Sandwich Islands, Pacific and Malaya); *Diodia* (America and Africa); *Borreria* (America, Africa, Asia and Australia); *Spermacoce* (Africa and America); *Staelia* incl. *Hypodematium* (Africa and South America); *Asperula* (Europe, Mediterranean, West Asia, India and Australia); *Galium* (almost worldwide in tropics and particularly temperate territories); *Rubia* (America, Asia, Africa and Europe).

Interpretations which are to be formed from these data depend on the theory of world evolution which one subscribes to. Very many biologists have seized Wegener's theory of continental drift since it appears to explain some otherwise inexplicably peculiar distributions (Hutchinson). Shape and comparative geology of the coastlines affords some convincing evidence. Many geologists and others (du Toit, 1937; Joly, 1930; Babcock, 1947; Moreau, 1952, etc.), have supported the hypothesis but recent tendencies are to deny drift altogether and even many of the postulated land bridges which were supposed to persist long after the continents divided. Evidence from phytogeography must wait for more certain information from the geophysicists. Wegener's theory postulates that during the palaeozoic the continents were very close together. N. W. Africa and Iberia were linked to Venezuela and the Appalachians; most of the East Coast of Sth. America was contiguous with Africa; Madagascar and India were close to East Africa. The Antarctic continent was very displaced and situated between

Africa, Australia and New Zealand. The Northern and Southern Continents were separated by the Tethys Ocean. The continents are estimated to have begun separating and drifting from the main mass in the Lower Cretaceous which is also the time given for the origin of the Angiosperms i.e. too early for the theory to help much in the explanation of the distribution of modern genera. A more widely held view is that the tropical habitat was very extensive formerly (there is adequate fossil evidence for this) and many genera had a very wide distribution. Very widespread extermination in the late Tertiary would explain many of the anomalies in present day distribution. Data which help in forming a classification are not forthcoming from distribution data but they are sometimes suggestive. The *Vanguerieae* are almost restricted to Africa and they possibly arose there thus supporting the fact that all the genera in that tribe are seemingly close and naturally related. The *Rubieae* are restricted to temperate climates with some species on high ground in the tropics. Many have in fact a bipolar distribution of the kind Du Rietz (1940) has discussed. He refutes widespread dispersal over long distances (excluding the agency of man and certain species whose fruits are well-known to be carried by ocean currents) even for plants with very light spores such as lichens and mosses. This is supported by island endemism e.g. the flora of Socotra which has an amazing number of endemic genera and species in all groups for an island so close to the mainland. He gives evidence against drift and favours land bridges to explain migrations. He explains bipolar plant distribution in two ways (a) transtropical migration and (b) differentiation of taxa simultaneously out of polymorphic ancestral syngameons as distinct from the origin of taxa in a given area and subsequently spreading. This simultaneous appearance of a species is equivalent to saying that evolution is occurring from the family downwards. The tribes *Hedyotideae* and *Anthospermeae* are also bipolar but contain many truly tropical species. Transtropical migration occurred when the tropics were much colder and temperate plants could thus spread. Later, increasing temperatures either eliminated these plants from the tropics or forced them on to high ground. Such cold periods occurred during the Quaternary glaciations. The migrations were held to take place down the Andes route.

11. Close morphological similarity between species placed in different tribes could be due to (a) convergence, (b) wrong plac-

ing of the species concerned, (c) significant relationship i.e. link species between related tribes. Many resemblances are noticeable when one is working on the family. Some are mentioned below. These similarities were rather puzzling on the old system but all the genera mentioned come in the *Rubioideae* as defined by new characters. *Declieuxia (Psychotrieae)* and *Neopentanisia (Knoxieae)* have a very similar fruit structure to each other and also to some species of *Galium*. *Borreria ocimoides (Spermacoceae)* is very similar to many species of *Oldenlandia (Hedyotideae)*. *Arcytophyllum (Hedyotideae)* has species resembling some *Otiophora* species. *Otiophora (Anthospermeae)* has species resembling *Fergusonia* species *(Psychotrieae)*.

IV. — Improvements which may be made to the Classification.

The improvements I have suggested are based on a rather limited study of the genera contained in the *Rubiaceae* but members from all the tribes which have been proposed (whether accepted or not) have been examined.

The delimitation of the family needs a little modification. The genus *Gaertnera* so often placed in the *Loganiaceae* because of the more or less superior ovary resembles members of the *Psychotrieae* in flower structure, stipules, habit, and anatomy and I would not hesitate to place it in that tribe. It has been mentioned that Bremekamp suggests that the *Henriquezieae* should be raised to family rank. The evidence for this is strong. The zygomorphic personate corolla is unlike anything else in the *Rubiaceae*, the seeds are exalbuminous as in the *Bignoniaceae*, the testa is characteristic, and moreover Erdtman (1952) states that the pollen is anomalous and unlike any other *Rubiaceae*. I think that this tribe can be justifiably separated off.

The division of the family into two subfamilies *Cinchonoideae* (in the wide sense) and *Coffeoideae* must be abandoned and a division into three or four new subfamilies utilised. I agree with Bremekamp that the tribes with raphide-containing species should make up one of these subfamilies *(Rubioideae)* but disagree over the actual content of it. The *Guettardoideae* are well-characterised by their almost non-albuminous seeds and peculiar fruits. I prefer to consider as one subfamily at present, the group of tribes which Bremekamp shares between the *Ixoroideae* and the *Cinchonoideae*

(in his sense). He characterises them as having a curiously pitted testa and a characteristic pollen mechanism respectively, but as I have previously shown many of the members with the pitted testa character also possess the characteristic pollen mechanism. If the pollen mechanism character is considered of major importance then the *Naucleeae* must be associated with the *Ixoreae* and neighbouring tribes together with a number of the *Cinchoneae*. Bremekamp removes only *Crossopteryx* and *Coptosapelta* from the *Cinchoneae* but there are other genera which have the same pollen mechanism as judged from dry material. In *Hymenodictyon* for example the clavate style is definitely in contact with the anthers and later rapidly elongates. I have not seen any specimens of *Corynanthe* but from the illustrations of the flower structure it is clearly similar. Bremekamp combines *Crossopteryx* and *Coptosapelta* to form a tribe and presumably would add the other two genera mentioned. I do not believe such a procedure is justifiable since only one character is used to associate them. Other characters I have examined do not confirm it. *Crossopteryx* and *Hymenodictyon* have 3-colpate reticulate pollen and the lumina of the testa cells are pitted as in *Cinchona;* moreover they are not aluminium accumulators. They resemble many *Cinchoneae* and *Naucleeae*. *Coptosapelta* has porate pollen with very open reticulation, non-pitted testa and all the species are aluminium accumulators. It is the only genus of the four which I consider should be removed from the *Cinchoneae*.

The *Rubioideae* can be subdivided into tribes fairly easily and some of these can be associated together. The three woody tribes *Psychotrieae, Morindeae,* and *Coussareeae* are similar in structure and I group them together. All have erect or nearly erect solitary ovules and porate pollen grains occur in all three (not exclusively). The aggregate fruits of *Morinda* and the very peculiar 2-porate pollen of the genus *Coussarea* are considered to be specialisations. The fruit is indehiscent and succulent or leathery in all and all three contain species which are very marked aluminium accumulators. Bremekamp has left the position of the genus *Schradera* doubtful but has referred it to a tribe of its own. I agree with him that raphides are present and that it must be removed from the *Mussaendeae* in which it was formerly placed and with which it has very little in common. I refer it to a position near the *Morindeae* with which it agrees in inflorescence. It has many specialised characters and is also specialised ecologically, being one of the few

epiphytic *Rubiaceae*. The *Urophylleae* are known to me only by their African representatives. I disagree with Bremekamp's statement that raphides are absent but admit that they are sparse in the leaf tissues but commoner in the fruits. I consider that this tribe should be placed in the *Rubioideae*. The morphological resemblance between some *Psychotrieae* (e.g. *Lasianthus*) and some *Urophylleae* (e.g. *Pauridiantha*) is strong e.g. habit, flower shape, and nature of the inflorescence. It is significant that raphides are almost confined to the fruit and ovaries in some species of *Lasianthus,* particularly the highly specialised ones endemics to the Uluguru Mountains. One character is not altogether in accordance with the transfer of the *Urophylleae* to the *Rubioideae*. The style is often slightly capitate and not bifid as is usual in the *Rubioideae* but several species of *Psychotria* have very similar styles and stigmas (see Pl. XVI, figs. F and G). I have pointed out that I do not consider this character alone to be of much importance. Other characters such as the presence of heterostyly in *Pauridiantha* are I think more important.

The genus *Craterispermum* has always been placed in the *Vanguerieae* (e.g. by Bentham and Hooker, Hutchinson and Dalziel, etc.), the position of the ovules and the general habit of the genus suggesting such a procedure. The general habit is, however, equally similar to many *Psychotrieae* and *Urophylleae* and I would remove this genus to a separate tribe placed near to them. There are many reasons for this decision. The species are heterostylous, the style is bifid and not capitate (Pl. XVI, f. A-D), and raphides are present in varying amounts. In a new and as yet undescribed species recently received from the Uluguru Mountains raphides are very abundant. These characters are not those of the *Vanguerieae*. All the species of *Craterispermum* have peculiar yellowish foliage and are marked aluminium accumulators. In the *Vanguerieae* only a few species of *Canthium* are accumulators. The pollen is porate as it is in both the *Vanguerieae* and the *Psychotrieae*. The *Craterispermeae* differ from the *Psychotrieae* in having pendulous ovules (4).

Bremekamp disagrees with Hutchinson and Dalziel who merge the *Knoxieae* and the *Hedyotideae*. I followed the same course

(4) Roberty (Bull. Inst. Français d'Afrique Noire *16*, 60-61 (1954) has placed *Craterispermum laurinum* in *Canthium*. This is greatly at variance with the truth but it is well-known that Roberty's views are completely unacceptable, being based on a set of artificial rules which the characters are made to fit.

when describing the genus *Neopentanisia* but now agree with Bremekamp that there are adequate reasons for keeping the two separate. The structure of the flower is certainly similar in the two tribes cf. e.g. *Pentas* with *Pentanisia* but then so it is in many members of all the tribes in the *Rubioideae*. A careful review of all the characters shows that there is a strong similarity between the *Knoxieae* and the *Psychotrieae*. The *Knoxieae* it is true are herbs though often very woody at the base whereas the *Psychotrieae* are predominantly shrubby. The fruits of many species of *Pentanisia* (particularly subgenus *Holocarpa* which are fleshy with pyrenes) are very similar to those of several genera in the *Psychotrieae*, e.g. *Triainolepis* and *Geophila*, the last a genus of herbs. The tendency to unequal sepals, marked in the *Knoxieae*, is noticeable in *Triainolepis*. The fruits and sepals of *Neopentanisia* show a close resemblance to those of the genus *Declieuxia (Psychotrieae)*. Both tribes are noticeable for their aluminium accumulating species and both have similarly reticulate pollen (Pl. XII, fig. D and Pl. XIV, fig. A). *Calanda* K. SCHUM., an Angolan genus redescribed much later by Chiovenda (who overlooked Schumann's work) as *Otocephalus* has been placed by some in the *Vanguerieae* and was found so-placed in the Kew Herbarium. I place it without hesitation in the *Knoxieae* since it shares many characters with the members of that tribe, herbaceous habit, solitary pendulous ovules, unequal calyx lobes, possession of raphides, strong aluminium accumulating properties and the similarity in structure of flower and fruit. It has certain floral peculiarities — two corollae are shared by one calyx and two ovaries. The ovaries are one-locular but joined in pairs, the calyces becoming one. *Neobaumannia* HUTCH. and DALZ. (= *Baumannia* K. SCHUM.) is placed in the *Hedyotideae* by its authors. The single species *N. hedyotidea* (K. SCHUM.) HUTCH. and DALZ. is also to be placed in the *Knoxieae* as Schumann suggested. The fruit is dry and separates into two cocci in a similar way to *Pentanisia prunelloides* WALP. and *Knoxia* itself.

I agree with Bremekamp that the *Coccocypseleae* should be referred to this subfamily and would place them near the *Paederieae* (on external general appearance only). The genus *Coccocypselum*, in habit rather like *Geophila (Psychotrieae)*, was formerly included in the *Mussaendeae* by virtue of its numerous ovules and berry fruit but raphides are abundant in the tissues. I have not seen enough material to look for heterostyly.

The *Anthospermeae, Spermacoceae,* and *Hedyotideae* form a group of tribes characterised by herbaceous or subshrubby habit and usually dry dehiscent fruits. The *Spermacoceae* also share characters with the *Rubieae* which are otherwise rather isolated in the subfamily — both tribes have pluricolpate pollen, a character which does not appear in any of the other tribes. The most characteristic structures in the *Rubieae* are the foliar stipules and polygonal stems with collenchymatous ribs. The *Argostemmateae* (formerly included in the *Hedyotideae*) are also isolated being delicate annual herbs with thin capsules. Their main diagnostic criterion « anthers joined in a cone » has two exceptions. I would place the tribe near to the *Hedyotideae*. Bremekamp does not mention the *Cruckshanksieae* possibly agreeing with K. Schumann that this tribe should be merged with the *Hedyotideae*. Bentham and Hooker associated this tribe with the *Retiniphylleae* to form one of the three series into which they divided the family as a whole. The only similarity between these two tribes is the possession of collateral ovules. Numerous characters are shared, however, between the *Cruckshanksieae* and the *Hedyotideae* — septate indumentum, hypocrateriform corolla, herbaceous habit, unequal sepals, possession of raphides, and pronounced heterostyly. I believe that these tribes should be placed next to each other or united but I have seen very few *Cruckshanksieae*.

I disagree with Bremekamp over the composition of his tribe *Ophiorrhizeae*. I have examined members of the three genera he includes — *Ophiorrhiza, Spiradiclis* and *Virectaria* (= *Virecta*). He states that raphides are absent in all but claims that all have the same type of testa composed of cells with thick walls ornamented with warts. I agree that such cells do occur in all three but have found raphides in the first two genera. Raphides are not present in *Virectaria* except in a species formerly included in the genus, *V. setigera* Hiern. This I have shown to be a *Parapentas* and a typical member of the *Hedyotideae* (Verdcourt, 1953). I do not regard the structure of the testa as reliable when there is a lack of macroscopic morphological agreement between *Virectaria* and *Ophiorrhiza,* save that both have a prominent disc. I would exclude *Virectaria* from the tribe which I refer to the *Rubioideae*. *Virectaria* is well-known to show a striking resemblance in habit and indumentum to *Sipanea (Rondeletieae)* — so close that the genera were once confounded. In my revision of *Virectaria* I incorrectly referred *Sipanea* to the *Hedyotideae* being misled by the

similarity between some species of *Sipanea* and *Otomeria*. Aestivation differences and the absence of raphides indicate that the similarity is probably of little significance. The similarity between *Virectaria* and *Sipanea* may also be accidental since there are testa and aestivation differences. *Virectaria* species have several characters which do not recur in any other genus of the family as far as I know. The fruit consists of a capsule one valve of which remains attached to the rachis by a stiff pedicel and one which is deciduous. The pollen is narrowly ellipsoidal with characteristic markings. This genus I would place in a tribe of its own which would occupy an isolated place in the *Cinchonoideae* (sensu lato).

I have been unable to study Bremekamp's *Pomazoteae* save for one species of each of the three genera *Pomazota, Lerchea* and *Xanthophytum* which were all described in the *Hedyotideae* but Bremekamp excludes them. He characterises this tribe by the thin - walled, more or less coarsely tuberculate testa cells. I have confirmed this character for *Pomazota*. True raphides are absent but small rod-like crystals of a very similar type occur in the tissues. The hairs are intermediate between incompletely septate and truly septate, the septae being rather numerous. There is some resemblance between *Pomazota* and *Virectaria* in indumentum, testa cells and particularly the disc. Both have a capsular fruit, numerous ovules and valvate aestivation. Fine rod crystals are present in *Xanthophytum* and in *Lerchea* the crystals are very similar indeed to raphides, particularly in the fruit. The hairs in *Xanthophytum* are incompletely septate and minute in *Lerchea*. I think these genera should be placed in the *Hedyotideae* but they form a link with the *Cinchonoideae*. I have been unable to examine fresh material and only very little dry material so my suggestion is tentative.

The genus *Deppea* has already been mentioned (page 231). I do not know where to put it in the *Rubioideae*. It contains sparse raphides not easy to see but has a contorted aestivation and pitted testa cells. The corolla is divided to the base as in the *Argostemmateae* and the capsular fruit is similar to those of many genera in the *Hedyotideae*. The genus is another link between the two main subfamilies.

Didymochlamys Hook. f. (a monotypic genus) is the only *Rubiacea* with alternate leaves, probably due to the suppression of one leaf at each node. Very unequal leaves occur at the nodes in some species of *Argostemma*. A microscopic analysis could not

be made but raphides appear to be present and I would refer the genus to the *Hedyotideae*.

I agree with Bremekamp that the *Guettardeae* are distinct enough to be placed in a separate family but I have only been able to study the solitary African member, a common littoral plant in Kenya, and a few other genera which have been borrowed.

The *Cinchonoideae* (including Bremekamp's *Ixoroideae*) contains a considerable number of tribes. The *Naucleeae* are well characterised by their compact globular inflorescences. They possess what I will for short call the « ixoroid pollen mechanism ». The fruit is succulent or dry and in the latter case the seeds are winged and show a clear similarity to those of the *Cinchoneae*. The other genera show resemblances to genera in the *Mussaendeae*. *Cephalanthus* with its solitary pendulous ovules is as Bremekamp points out rather anomalous but I would not remove it from the tribe since it clearly resembles the other genera in general habit, corolla shape and inflorescence structure. The testa cells of all the genera I have examined are pitted. The *Cinchoneae* have capsular fruits, winged seeds and a usually lax terminal inflorescence. The testa cells have large pits in the lumina. Bremekamp has removed a certain group of genera formerly placed in this tribe to the *Rubioideae-Hedyotideae*, namely *Bouvardia, Heterophyllaea, Hindsia, Danais, Manettia, Coursiana,* and *Hymenopogon*. Baillon long ago suggested the same procedure for some of the genera. Since numerous ovules and capsular fruits are a feature of both tribes the only character associating them with the *Cinchoneae* is the possession of winged seeds. I agree that this character by itself is of little importance. Raphides are found in all the genera mentioned and the testa cells are not pitted. From a general morphological standpoint these genera have more characters in common with genera in the *Hedyotideae* than they have with those in the *Cinchoneae*. There is for example a similarity between the fruits of *Hindsia* spp. and *Pentas* (subgen. *Megapentas*) spp. (Pl. XVI, figs. W and X). Cultivated *Bouvardia* spp. are easily confused with *Pentas* spp. During a rapid survey of all the *Rubiaceae* preserved at Kew I noted that the members of the Madagascar genus *Schismatoclada* Bak. were heterostylous. This genus was placed in the *Cinchoneae* by its describer and this would be in accordance with the old classifications since the seeds are winged. As no other members of the tribe showed heterostyly I borrowed material of the genus in order to make a more detailed

study. Raphides were found to be present in the tissues and I transfer this genus to the *Hedyotideae*. There are no characters which oppose this transfer, the aestivation is valvate, the ovules numerous, the capsule beaked and the pollen 3-colpate and reticulate. I have examined the testa and the pits which are characteristic of the true *Cinchoneae* are entirely lacking (Pl. XVI figs. T and V). Hairs are present in the throat of the corolla in some of the species and absent in others, but there is no external indumentum. The foliage which is reminiscent of *Psychotria* has the yellowish appearance often found in aluminium accumulators. Baker entirely overlooked the heterostyly and it is evident to me that *S. psychotrioides* BAKER is merely a thrum-eyed form of the pin-eyed *S. trichopharynx* BAKER. Baker overlooked heterostyly in other genera e.g. *Oxygonum (Polygonaceae)* where he again separated species by the exsertion or otherwise of the stamens.

The *Rondeletieae* are well-characterised by their capsular fruits containing large numbers of minute horizontal seeds. The testa cells are pitted and the aestivation not valvate. The *Condamineeae* are very similar but the aestivation is valvate and the seeds often winged. In both the habit is mainly arborescent and the stipules are entire or at the most bifid. I would combine these two groups into one tribe and consider them to be subtribes at the most. In the *Cinchoneae* placed next to them the aestivation character is considered valueless by all previous workers because if used it would divide an otherwise compact tribe — all three types of aestivation occurring in it. I do not think this one character is sufficient to separate the *Rondeletieae* and *Condamineeae* particularly as two types of aestivation occur in the *Rondeletieae*. Resemblances to the *Hedyotideae* are shown by the herbaceous *Sipanea* and *Limnosipanea;* the genus *Deppea* already discussed seems intermediate in many ways. Bremekamp suggested that it might be placed near to the genus *Hamelia* but he had seen neither fruit nor seeds. I have found few characters in common and cannot agree with him.

The *Mussaendeae* (as delimited by Bremekamp with the *Urophylleae* removed and also certain other ecologically specialised genera such as *Mycetia* and *Myrioneurum,* both of which contain raphides, removed to the *Hedyotideae* despite the more or less succulent or very tardily dehiscent fruits) are morphologically similar to the *Condamineeae* + *Rondeletieae*. The main difference is to be found in the fruit which though of very similar structure

is with the sole exception of *Pseudomussaenda* succulent or leathery and indehiscent. *Pseudomussaenda* species have capsules but are otherwise very similar to *Mussaenda* and I consider Wernham's removal of the genus to the *Condamineeae* unnecessary. The aestivation is valvate in the *Mussaendeae*.

The *Gardenieae* after a group of genera have been removed to the *Ixoreae*, form a tribe characterised by the leathery indehiscent fruit with numerous seeds immersed in a pulp. The testa cells I have examined have mostly been devoid of sculpture but obscure pits are visible in some species. Some genera have unisexual flowers and some species have the pollen retained in tetrads. I have not been able to examine many extra-African members of this large tribe. I agree with Bremekamp that *Posoqueria* will have to be excluded but do not know where it should be put. It has a higher chromosome number than has been reported for any other *Rubiacea*, peculiar horny anthers like some *Apocynaceae* and it does not show the Ixoroid pollen mechanism that other members of the tribe possess. The *Ixoreae* are similar to the *Gardenieae;* they have the ixoroid pollen mechanism, succulent drupaceous fruits with few or solitary ovules in the loculi, and simple stipules.

The *Vanguerieae*, I consider, are a most natural tribe its members being in all probability genetically related. They have a facies which is immediately recognisable. The capitate or cylindrical « stigma », axillary inflorescences, valvate aestivation, solitary pendulous ovules, succulent fruit, porate unsculptured pollen grains and entire stipules are constant features (Pl. XV fig. F and Pl. XVI figs. A and B). The naturalness of this tribe is accentuated falsely, since the genera which have been described are separated by fewer characters than in some tribes. I consider that several genera will have to be placed in synonymy. The genus *Pygmaeothamnus* Robyns I would sink into *Canthium* as a section characterised by large fleshy fruits. Robyns established this genus for a South African pyrophyte, woody but under one foot tall. Bullock later described a new species from Tanganyika, *P. concrescens* and at the same time pointed out that the inflorescence characters partly used by Robyns to establish his new genus did not hold and that the only distinguishing character left was the small habit. In *Canthium* there is a species *C. crassum* Hiern which has large fleshy fruits and is identical in leaves, bark and flowers with *P. concrescens* Bullock. It differs only in being a large shrub (10 ft.) but is significantly, a plant of fireswept grasslands. Bearing

in mind the fact that there are scores of African woody genera (e.g. *Combretum, Terminalia, Ochna* and *Maerua)* which have evolved small numbers of very small pyrophytic plants, I unhesitatingly sink *Pygmaeothamnus* into *Canthium*. There are more characters in common between the two *Pygmaeothamnus* species and *Canthium crassum* than there are between *C. crassum* and its congeners. *C. crassum* and the two *Pygmaeothamnus* are some of the very few *Vanguerieae* which show aluminium accumulation.

I agree with Bentham and Hooker in placing the *Chiococceae* near to the *Vanguerieae*, both tribes agreeing in the morphology of their flowers, foliage and fruits (Pl. XVI figs. I and J). Raphides are absent in both and the ovules are solitary and pendulous. I have only been able to examine a few species. The pollen differs, that of *Chiococca* being ellipsoidal, narrowly 3-colpate but unsculptured. Bentham and Hooker, and K. Schumann maintain a tribe *Alberteae* which they place near the *Vanguerieae*. The genera have several things in common — contorted aestivation, solitary ovules in 2 locules, situated at the apex or above the middle of the loculus, coriaceous 2-locular fruits and a superior radicle. All are moreover African. Bentham and Hooker then divide the tribe into two groups, the first with axillary inflorescences comprising *Cremaspora, Polysphaeria, Belonophora, Aulacocalyx,* and *Rhabdostigma,* the other with terminal inflorescences and 1-4 of the calyx lobes accrescent, comprising *Alberta* and *Nematostylis*. Bremekamp on the other hand took out from this series of genera those characterised by the ixoroid pollen mechanism and referred them to a tribe *Cremasporeae,* excluding *Alberta, Nematostylis* and *Belonophora*. I agree with this breaking up of the *Alberteae* but would not keep up the tribe *Cremasporeae*. They differ from the *Ixoreae* only in minor ovule differences and could readily be accommodated in that tribe as a subtribe. It is well-known to all those who have to name African plants that confusion between the genera *Cremaspora, Polysphaeria, Coffea* and *Tricalysia* is easy on external morphological characters and it always puzzled me how these four genera could be distributed in three different tribes and two different subfamilies. I place all four in the *Ixoreae*. Bullock (1934) has confirmed this with regard to one genus. He shows that there are no real generic differences between *Kraussia* and *Rhabdostigma*. Bentham and Hooker placed *Kraussia* in the *Gardenieae* but it belongs to that group of the tribe which Bremekamp has transferred to the *Ixoreae* though he does not specifically mention it.

The fruits are drupaceous and the seeds are not immersed in pulp. In general habit it is very close to *Tricalysia* and I refer it to the *Ixoreae*. *Alberta* and *Nematostylis* I would leave as a tribe, the *Alberteae*, but only the former genus is known to me. They differ from the *Ixoreae* in the structure of the corolla but should be placed near that tribe. Bremekamp states that they do not show the ixoroid pollen mechanism but from my observations on dry material the style definitely elongates after the buds open but the « stigma » is thin and bears no pollen in all probability. It could be an example of the pollen mechanism degenerating. Two genera described after the publication of the « Genera Plantarum » have been referred by their authors to the *Alberteae* viz. *Lamprothamnus* HIERN and *Heinsenia* K. SCHUM. I have examined both of these, the first of which occurs in the coastal areas of East Africa and the second in the Usambaras and other montane rain forests. The structure of the corolla of *Lamprothamnus* is very similar to that of *Tricalysia* being funnel-shaped, bearded and 6-7 lobed (4-8 in *Tricalysia*). The flowers are bracteolate in both but subterminal in *Lamprothamnus* rather than axillary. *Tricalysia* has several pendulous ovules in the locules of the ovary; *Lamprothamnus* has one. Both have the ixoroid pollen mechanism. The pollen grains of *Tricalysia* spp. and *Lamprothamnus zanguebaricus* HIERN (the only species) are almost identical in every way (Pl. XV, fig. B) and I would refer the genus to the *Ixoreae* without question. *Heinsenia* on the other hand has a bell-shaped corolla quite different from that of *Lamprothamnus* and the anthers are not attached at the throat as in typical *Ixoreae*. Many genera in the *Gardenieae* have similarly shaped corollae. The fruit, inflorescence and ovary agree with the *Ixoreae* however and I would refer this genus to a new subtribe of the *Ixoreae* differing in the position of the anthers. From descriptions I think it possible that some of the genera referred to the *Gardenieae* by Bentham and Hooker which I have not seen and which do not have the characteristic fruit of the true *Gardenieae* will have to be placed here.

Three tribes remain to be discussed. The *Hamelieae* are I believe entirely artificial, I agree with Bremekamp that the nominate genus *Hamelia* contains raphides. The one character which makes it difficult to place the genus in the *Rubioideae* is its imbricate aestivation. It would have to be one of very few exceptions to the rule that the *Rubioideae* have a valvate aestivation. I would however place the genus in that subfamily to occupy an isolated position

possibly near to the *Ophiorrhizeae* which are similar in the structure of the corolla and disc. The external indumentum in *Hamelia* consists of septate hairs. I have not seen enough material of the genus to pronounce on the presence of heterostyly. *Heinsia* is entirely different from *Hamelia* in habit, corolla shape and external indumentum. Raphides are not present and the testa cells have definite pits (Pl. XVI, fig. M). It clearly belongs in the *Cinchonoideae*. The aestivation is similar to that of the *Gardenieae* but the seeds are dry, small and angular and not immersed in pulp. The fruit closely resembles those of the *Mussaendeae* and *Rondeletieae* in structure and is indehiscent as in the first tribe. *Heinsia densiflora* HIERN is similar in flowers and foliage to *Mussaenda* spp. and both show incomplete heterostyly. I regard the genus as referable to a subtribe of the *Mussaendeae*. I have mentioned before that I do not consider aestivation to be of much importance in the *Cinchoneae* group of tribes. *Bertiera* differs similarly from *Hamelia* in having no raphides and a different corolla and external indumentum. I have found the testa cells to be pitted as in *Heinsia* and I would associate it with that genus. It is not difficult to find affinities between this genus and others in the *Cinchoneae* group of tribes e.g. *Sabicea* in the *Mussaendeae* s.s. Two species of *Bertiera* have inflorescences similar to those found in the *Naucleeae*. I have not been able to examine other genera referred to the *Hamelieae*.

The *Catesbaeeae* and *Retiniphylleae* are New World tribes and I have examined a few representatives of both. Raphides are absent in both cases and both tribes are referable to the *Cinchonoideae*. The fruit and testa structure excludes them from the *Cinchoneae* group of tribes. The *Catesbaeeae* have a valvate aestivation and are for the most part spiny shrubs. The fruit is fleshy and the seeds agglutinated, the testa rugose but not pitted. I would place them near the *Gardenieae*. The *Retiniphylleae* have a contorted aestivation and a fleshy fruit with 5-7 pyrenes. The ovules are collateral. The former association of this tribe with the *Cruckshanksieae* by Bentham and Hooker has already been mentioned. I believe that the *Retiniphylleae* are to be placed near to the *Ixoreae*.

The comments of this section may be summarised in tabular form. It is intended as a working classification and needs testing with the floras of other areas, since neither Bremekamp nor I have

examined more than a fraction of the genera in the family thoroughly. Further work can not but help produce modifications. A linear classification obscures many affinities but is the only practical one for arranging specimens and lists. I have followed Bremekamp in the content of the subfamilies with the following exceptions — *Schradereae, Urophylleae, Craterospermeae, Hamelieae, Ophiorrhizeae, Cruckshanksieae, Catesbaeeae,* and *Retiniphylleae* which he either did not deal with or left unplaced. I also vary from him in sinking the *Condamineeae* into the *Rondeletieae,* and considering the *Cremasporeae* a subtribe of the *Ixoreae.* The order of the tribes is mine and also my treatment of the subtribes I have based on *Heinsenia* and *Heinsia.*

FAMILY RUBIACEAE (5)

A. Raphides present and seeds albuminous.

Subfamily *Rubioideae :* Trees shrubs or herbs predominantly herbaceous save for the first three tribes and the subsequent three newly erected tribes. Aestivation valvate with very rare exceptions: *Hamelia* (imbricate), *Deppea* (contorted) and *Hillia* (contorted). Indumentum on stem, leaves, etc., very often septate. Complete heterostyly frequent. Ovules solitary or numerous, erect or pendulous in 1-∞ locules. Fruits dry or succulent, dehiscent or indehiscent. Stipules frequently fimbriated. Style usually divided into two linear lobes bearing the stigmatic papillae on their inner surfaces. Testa cells rarely pitted.

Tribe *Psychotrieae :* Mostly shrubby, rarely herbs or trees. Ovules solitary in the 2-8 locules, erect. Fruit usually succulent containing 2-8 pyrenes, more rarely dry and separating into cocci. Pollen porate.

Tribe *Coussareeae :* Shrubby, ovary mostly 1-locular, ovules 2, erect. Fruit leathery 1-seeded. When 2-locular the septum is evanescent.

Tribe *Morindeae :* Trees or shrubs. Ovary 2-locular, rarely 4, ovules solitary in the locules affixed at or below the middle. Fruit baccate or drupaceous, 2-4-locular or containing pyrenes. Pollen porate.

Tribe *Schradereae :* Epiphytic shrubs, ovary 2-4-locular, ovules numerous. Flowers in bracteate heads. Fruits succulent.

Tribe *Urophylleae :* Shrubby or arborescent rarely herbaceous. Ovary 2-∞ locular, ovules numerous. Raphides thicker than in other tribes. Fruit baccate, 2-∞ locular, many-seeded. Pollen colpate with large pores.

Tribe *Craterispermeae :* Shrubby or arborescent. Ovary 2-locular, ovules solitary, pendulous. Fruit baccate 1-2-locular. Pollen porate.

Tribe *Knoxieae :* Herbaceous (or small subshrubs). Ovary 1-5-locular, ovules solitary, pendulous. Fruit either succulent with pyrenes, dry and indehiscent or dividing into indehiscent cocci.

N. B. — The above tribes form a series and all contain aluminium accumulators — in fact the majority of the marked Rubiaceous accumulators are contained in them.

(5) For validification of new names, see appendix 2, p. 280.

Tribe *Paederieae :* Usually foetid climbers. Ovary 2-5-locular, ovules solitary, erect. Fruit 2-coccous with thin epicarp or capsular.

Tribe *Coccocypseleae :* Creeping herbs. Ovary 2-locular, ovules numerous. Inflorescence bracteate, fruit baccate.

Tribe *Argostemmateae :* Fragile herbs. Ovary 2-locular, ovules numerous. Stamens with anther cells connivent, with two exceptions, opening by apical pores. Fruit a leathery or membranous capsule dehiscing apically. One leaf in pair often reduced. Corolla rotate divided almost to the base.

Tribe *Ophiorrhizeae :* Herbs, ovary 2-locular, ovules numerous. Disc fleshy. Capsule very characteristic, broadly obcordate. Not heterostylous.

Tribe *Hamelieae* (s.s.) : Shrubs. Aestivation imbricate. Ovary 5-locular, ovules many. Disc fleshy. Fruit baccate.

Tribe *Cruckshanksieae :* Herbs. Ovary 2-locular, ovules two in each loculus, affixed to the middle of the septum. Fruit capsular.

Tribe *Hedyotideae :* Herbs or shrubs. Ovary 2-locular rarely 3-4, ovules usually numerous rarely few or solitary, affixed to the base of the septum. Fruit capsular. (The genera *Mycetia* and *Myrioneurum* have tardily dehiscent or indehiscent fruits but are placed here by Bremekamp. They were not available to me. The genus *Deppea* has been mentioned in the text.)

Tribe *Anthospermeae :* Herbs or shrubs. Many genera have unisexual flowers. Ovary 1-4-locular, ovules solitary in each loculus, erect. Fruit dry dividing into cocci or capsular.

Tribe *Spermacoceae :* Herbs. Ovary 2-locular (rarely 3-4), ovules solitary in the locules, affixed to the middle of the septum. Fruit dry, capsular or dividing into cocci. Pollen pluricolpate.

Tribe *Rubieae :* Herbs of temperate climates. Stipules with few exceptions (some *Galia,* and *Didymaea*) foliar. Stem polygonal with collenchymatous ribs. Ovary 2-locular, ovules solitary in the loculi, attached to the septum. Fruit fleshy, didymous.

N. B. — The genus *Hillia* has raphides, and tufts of hairs on its seeds but the aestivation is contorted. It probably needs a special tribe but the writer has not seen it.

B. Raphides absent (if calcium oxalate present then in the form of crystal sand, etc.). Seeds albuminous. Hairs never truly septate.

Subfamily *Cinchonoideae* (including Bremekamp's *Ixoroideae*) : Trees and shrubs rarely herbs. Aestivation various. External indumentum usually of thick-walled non-septate or incompletely septate hairs. Complete heterostyly does not occur. Ovules solitary or numerous, attached to the septum or pendulous in one to many locules. Fruits dry or succulent, dehiscent or indehiscent. Stipules usually undivided. Style fusiform, capitate or divided into linear lobes. Testa cells in the first few tribes conspicuously pitted.

Tribe *Naucleeae :* Trees or climbers. Flowers aggregated into spherical heads. Ovary 2-locular, ovules numerous (rarely solitary, in *Cephalanthus*). Fruit a succulent syncarpium or collection of capsules. In the case of capsular fruits at least, the testa cells are pitted. Ixoroid pollination mechanism present.

Tribe *Cinchoneae :* Trees or shrubs. Ovary 2-locular, ovules very numerous, vertical or ascending. Fruit capsular, testa of seeds with pits. In some genera the ixoroid mechanism occurs. Seeds winged.

Tribe *Rondeletieae* (including *Condamineeae*) : Trees or shrubs rarely herbs. Aestivation various, valvate in the subtribe *Condamineinae*. Ovary 2-locular, ovules very numerous, horizontal. Fruit capsular, seeds mostly not winged, testa pitted. Ixoroid mechanism absent.

N. B. — The aberrant genus *Virectaria* with its characteristic capsules has been discussed in the text.

Tribe *Mussaendeae* : Mostly trees and shrubs. Aestivation valvate save in some species of *Isertia* and in the subtribe *Heinsiinae* where the aestivation is imbricate. Ovary 2-∞-locular, ovules numerous. Fruit fleshy or dry, indehiscent (with the exception of *Pseudomussaenda* which has capsular fruits). Seeds minute not winged, angular, testa pitted. Ixoroid mechanism absent.

Tribe *Catesbaeeae* : Shrubs or trees. Aestivation valvate. Ovary 1-2-locular, ovules usually numerous attached to a placenta adnate to the septum, parietal or inserted near the apex. Fruit fleshy or leathery. Seeds usually agglutinated. Testa not pitted.

Tribe *Gardenieae* : Trees or shrubs. Aestivation contorted or imbricate. Ovary 1-∞-locular, ovules numerous or few per loculus. Fruit with a woody or leathery pericarp, seeds embedded in a gelatinous mass. Testa rarely pitted. Some genera have the pollen in tetrads. Unisexuality occurs. Ixoroid pollination mechanism present.

Tribe *Ixoreae* (with subtribes *Cremasporinae* and *Heinseniinae*) : Trees or shrubs. Aestivation contorted. Ovary 2-locular, ovules one to few attached to a fleshy placenta affixed near middle of septum. Fruit a drupe with thin endocarp. Testa not pitted. Pollination mechanism ixoroid. Anthers inserted at throat, just exserted, often twisted. Radicle inferior.

Subtribe *Cremasporinae* differs only in the solitary ovules placed apically in the locules and the superior radicle.

Subtribe *Heinseniinae* differs in the position of the anthers which are included.

N. B. — The genus *Coptosapelta* which belongs near here has been discussed in the text.

Tribe *Retiniphylleae* : Trees or shrubs. Aestivation contorted. Ovary 5-7-locular, locules with two ovules. Fruits fleshy with 5-7 pyrenes.

Tribe *Alberteae* s.s. : Trees or shrubs. Ovary 2-locular, ovules solitary, pendulous from the apex. Radicle superior. Fruit leathery, 2-locular. Stigma elongating after bud opens. See text.

Tribe *Vanguerieae* : Shrubs or trees, more rarely woody-based herbs. Aestivation valvate. Ovary 2-locular, ovules solitary, pendulous. « Stigma » cylindric or capitate. Fruits fleshy containing pyrenes. Ixoroid mechanism present. Stamens inserted at throat. Pollen porate, unsculptured.

Tribe *Chiococceae* : Shrubs or trees. Aestivation valvate or imbricate. Ovary 2-10-locular, ovules solitary, pendulous. Stigma mostly clavate. Fruits mostly fleshy with 2 pyrenes. Stamens inserted near the base of corolla tube.

C. Raphides absent, seeds exalbuminous or with traces only of albumen.

Subfamily *Guettardoideae*.

Tribe *Guettardeae* : Trees or shrubs. Aestivation imbricate or valvate. Indumentum not truly septate. Heterostyly not known to occur but style grows as flower matures in some species. Ovary 2-∞-locular, ovules solitary, pendulous. Fruit drupaceous or with woody putamen, with 2-pyrenes, rarely dicoccous. Seeds with little or no albumen. Testa not sculptured or irregularly reticulate. Pollen porate.

It is not pretended that every genus will be able to be fitted into this scheme with much more ease than into the older ones.

Certain genera are puzzling e.g. *Jackia*, but it is claimed that it is more natural than the older ones and more useful. Not until a very complete survey of all the genera (and many need recollecting) has been made will a really adequate system be divised.

V. — Phylogenetic considerations.

A very excellent summary of the relation between taxonomy and phylogeny is given by Turrill (1942) and he summarises the criteria which have been used to determine primitiveness.

It may be said at once that this section is based on conjecture. The only concrete evidence for phylogeny is fossil evidence. K. Schumann (1891) cast doubt on all the fossils which had been referred to the family up to that time. Neither pollen nor fruits appear to have been found in any of the well-known deposits, with the exception of the temperate genus *Galium*.

The geographical distribution of the family has already been mentioned. The family may be divided into groups having different distribution patterns.

1. Tribes almost confined or quite confined to one continent or area — have developed locally or become extinct in other places. *Vanguerieae, Argostemmateae, Alberteae, Catesbeaeeae, Coccocypseleae, Cremasporeae, Retiniphylleae, Coussareeae* (one in Africa), and *Schradereae.*
2. Tropical tribes not represented in Africa. *Rondeletieae* (including *Condamineeae*) and *Chiococceae.*
3. Tropical tribes not represented in South America. *Ophiorrhizeae, Urophylleae* and *Knoxieae.*
4. Tropical tribes widely distributed but not in Australia. *Mussaendeae* and *Cinchoneae.*
5. Widespread throughout the tropics. *Psychotrieae, Morindeae, Guettardeae, Gardenieae, Ixoreae* and *Paederieae.*
6. Tribes occuring in both the tropics and temperate regions and on isolated islands. *Hedyotideae, Spermacoceae, Anthospermeae* and *Rubieae.*

It seems possible that groups 5 and 6 are the oldest. The others may be just as old but more local or they may be recent. The age and area theory of Willis, really meant to apply only to ten or more related species of one genus, is not universally applicable (Babcock, 1947) but in the *Rubiaceae* or at least some groups of them, the idea that antiquity and area of distribution are correlated may be of some value since the seeds are not adapted to rapid dispersal. Species with winged seeds or edible fruits occur in both

local and widely distributed groups. It is certain that a rain forest habitat and associated species were widely distributed in the Tertiary and that this tropical flora has become more localised as cool climates spread in later epochs. Many groups were probably cosmopolitan and owe their present distribution to later widespread extinction.

Some floras are held to be more ancient than others e.g. the flora of Socotra with its numerous endemics is undoubtedly old but it does not throw much light on primitiveness. *Dirichletia* and *Placopoda* are shrubby *Hedyotideae* with few ovules. The usual *Oldenlandia* spp. are present and a very anomalous *Pseudomussaenda*. At one time it was held (Thistleton Dyer et al.) that all floras originated in the north and that the Australian flora is an ancient one formed in the north as early as the late Cretaceous (!) and that it migrated in prepleistocene times during the glaciations. Sinnot thinks that the migrations must be recent else all bipolar genera would be changed by isolation. This has happened in some e.g. the southern *Asperulae* are dioecious. Sinnot and Bailey (1914) regard endemic elements as ancient since they are either remnants of a flora which died out elsewhere or they originated in the area — a long process in either instance. They also deduce that the herbaceous habit is advanced and that it has developed on many occasions. They claim that the most ancient floras e.g. of Australia, St. Helena, Polynesia, Galapagos Islands, etc., are predominantly woody. Herbs are dominant in temperate zones and woody plants in the tropics where the ancient vegetation type tropical rain forest is predominant (or was). This holds for the *Rubiaceae* where in temperate zones the species are 100 % herbaceous but in the tropics only 19-30 % are herbaceous. Herbs have been developed in the north and south as an answer to progressive refrigeration and more rarely in the tropics as an answer to specialised conditions.

Long lists of « criteria of primitiveness » are given by Hutchinson (1926) and Bessey (1915) (see summary by Turrill, 1942). These are scarcely ever based on evidence but on convictions and guesses, admittedly of persons who have a wide and comprehensive knowledge of the plant kingdom. Neither Hutchinson nor Bessey indicate that they took into account the work done on the London Clay flora and other fossil floras. Those criteria which have a bearing on the evolution of the *Rubiaceae* are as follows : woody habit, perennial habit, non-epiphytic habit, non-scandent habit, hermaphrodite flowers, solitary flowers, presence of endosperm,

simple fruits and dry fruits are considered primitive and their opposites advanced. Different characters evolve differently in different directions and at different rates and all organisms will have a mixture of primitive and advanced characters. Series may be made out showing the evolution of a character amongst recent plants (i.e. the end products of lineages) but without fossil evidence there is difficulty in assigning directional values. It is possible for a species recently separated to have more primitive characters than a more ancient one. Hutchinson does not preclude the possibility of the herbaceous habit occasionally being more primitive than the woody habit and this applies to the other characters. Accepting these criteria the *Guettardoideae*, *Cinchonoideae* and part of the *Rubioideae* have the primitive character of woody habit, indicating that two thirds of the *Rubioideae* are the most advanced members of the family. The perennial habit is linked with the woody habit — only a few of the herbaceous *Rubioideae* are annuals and a very few *Cinchonoideae*. Scandent plants occur in both the *Cinchonoideae* (*Naucleeae, Vanguerieae, Ixoreae*, etc.) and the *Rubioideae* (*Paederieae* mostly scandent, *Hedyotideae*, etc.) and are advanced plants in their particular tribes. There are a few epiphytes in the family, *Schradera (Schradereae), Myrmedoma, Myrmephytum, Squamellaria, Hydnophytum, Myrmecodia*, etc. (all *Psychotrieae* having ants living in symbiosis in tubers at the base of the stem) and these are also to be considered advanced plants. Where solitary flowers occur in the family (e.g. in some *Rytigynia*) they are axillary and obviously the result of reduction. Unisexual flowers occur in a few *Gardenieae*, very few *Rubieae*, and many *Anthospermeae*. I regard all these plants as derived from bisexual members of the tribes. In the *Rubieae* only a very few *Asperulae* are unisexual; the species in other regions outside Australia, the vast majority, are bisexual. Unisexuality is more frequent in the *Gardenieae* and *Anthospermeae* and in these, rudimentary organs of the missing sex are often to be found in the flowers. In the *Anthospermeae* male and female flowers are sometimes separate but often the flowers are bisexual but heterostylous. In *Anthospermum herbaceum* L. F. plants of the « stigmas exserted » form are found which are « extra female » having the stigmas very long and conspicuous and the anthers sterile. I believe that unisexuality in this tribe might have arisen via heterostyly. Only one tribe, the *Guettardeae*, have seeds without endosperm and are thus advanced in this respect having been derived from ancestors possessing it.

Traces remain in some species. Aggregate fruits are found in the genus *Morinda* and some *Naucleeae*. Dry fruits occur in a large number of genera. Parts of all three subfamilies are characterised by them. The *Psychotrieae* and *Ixoreae* groups of tribes have succulent fruits. Corner (1950) has very convincingly shown that the early spermatophytes were trees of the rain forest having massive fruits and pendulous red arillate seeds. None of the *Rubiaceae* as far as I am aware possess this character or remnants of it.

Sporne (1948, 1949) has recently developed a method which gives a very convincing assessment of primitive criteria. He shows that two advanced or two primitive characters will occur together more frequently (i.e. are correlated) than they would be if distributed at random throughout the plant kingdom. He worked out numerous correlations and decided whether or not the characters were advanced or primitive by referring to the plants identified by Reid and Chandler in the London Clay. He reached the conclusion that the ancestral dicotyledon was woody, had alternate leaves with stipules and glands; its flowers were unisexual, actinomorphic and polypetalous with many stamens and carpels; the seeds were arillate and had two vascularised integuments. Woody habit is thus confirmed as primitive. Sporne disagrees with Hutchinson concerning the sexuality of the primitive flower but in the case of the *Rubiaceae* I believe, for the reasons given above that unisexuality is secondary. The other characters help little with the estimation of the relative primitiveness of the groups contained in the *Rubiaceae*. They show that the family as a whole is fairly advanced, Sporne giving it an « advancement index » of 67 % (this would be a little different with the *Henriquezieae* removed from the family since it would eliminate the character of zygomorphy). Sporne's methods could be applied to the particular characters I have listed as being of value in the classification of the *Rubiaceae*. Correlations for these could be worked out for all the families of dicotyledons and the results applied to the *Rubiaceae*. The necessary facts are not recorded for all the families and they would need re-examining.

Some of the facts concerning aluminium accumulation have been mentioned (p. 233). The subject is of interest in view of the fact that Chenery (in litt.) is of the opinion that aluminium accumulators « are primitive forms and may be senescent as well ». « Large genera which contain both accumulators and non-accumulators are in an active state of speciation ». This is of course speculative but

it is interesting to note that in the genus *Pentanisia* the hypothesis supports the phylogenetic tree derived from other fragmentary evidence and by guesswork (see Verdcourt, 1952). Chenery has kindly reported on various species of *Pentanisia* which I sent him as follows :

Non-accumulating species ...	*P. parviflora* (annual), *P. ourano-gyne.*
Slightly accumulating	*P. foetida, P. longituba.*
Accumulators	*P. schweinfurthii, P. prunelloides.*
Marked accumulators	*P. arenaria, P. procumbens, P. angustifolia, P. confertifolia.*

If these results are compared with the tree it will be seen that the greatest accumulators are near the bottom. They nearly all have thick woody rootstocks and are pyrophytes. The other species have thinner rootstocks or are even annuals. This correlation may be coincidental and needs checking against other accumulating genera which have been accurately revised and « family trees » proposed. The presence of aluminium may be a good indicator of age but the absence of it may not prove the converse. Using the twelve characters Sporne shows are primitive, a rapid check shows that only one correlation is likely. Nearly all accumulators are woody plants. Only rarely are all the members of a family accumulators. Only three families to which Sporne gives an advancement index of less than 35 contain accumulators and then only a few genera. It is of course possible that it is a primitive character which has been lost in all but a few families. In the *Rubiaceae* the group of tribes including and allied to the *Psychotrieae* are undoubtedly the most marked accumulators, and they are woody plants concentrated in moist forest areas and have a wide distribution throughout the tropics. Raphides do not occur in any of the families which Sporne concludes are primitive and the character does not appear to correlate with other primitive characters.

One of the first things to be considered is whether or not the family is monophyletic. The family is well-characterised and all the components morphologically rather similar and probably genetically related. Moves have been made to separate off the *Rubieae* as a separate family (see p. 212). It really implies that the rest of the tribes are more similar to each other than any of them is to the *Rubieae*. There is evidence both for and against this but mostly

against. The *Rubieae* show habit similarities with the rest of the tribes in the *Rubioideae*. The presence of raphides and the similarity between their pollen and that of the *Spermacoceae* are important ones. It is admitted that the *Rubieae* have distinct and peculiar characteristics of their own such as the foliar stipules and the polygonal stems with collenchymatous ribs. It is an interesting example of convergence that the most advanced family of dicotyledons *Labiatae* (fide Sporne) have pluricolpate pollen and polygonal stems with collenchymatous ribs. It has been doubted whether the stipules in the *Rubieae* are true stipules but rather supernumerary leaves. The morphology and anatomy of the nodes shows that the traditional interpretation is correct. Only two leaves in the whorl have axillary buds and are therefore true leaves. The rudiments of the remaining « leaves » arise at the growing point later than those of the two true leaves and between them. These stipular rudiments gradually catch up in their development. It is of interest to note that in one genus *Didymaea* HOOK. F., which by virtue of its habit and square stem is undoubtedly correctly placed near to *Rubia*, there are ordinarily opposite leaves such as occur in the other tribes. Certain species of *Galium* itself are similar. There is no real reason for considering the *Rubieae* as deserving of family rank. There would be equal specialised reasons for separating off the *Coussareeae*. I believe that the family is monophyletic in so far as that term means anything.

There are two views as to the derivation of the *Rubiaceae*. Wernham, Wettstein, etc., hold that the *Umbelliferae* are the parental stock and Utzschneider claims that the *Loganiaceae* are. The *Umbelliferae* have alternate leaves, and an inferior 2-locular ovary with solitary pendulous ovules. The *Loganiaceae* have opposite leaves, a more or less superior ovary with 2-4 locules and the ovules may be numerous or solitary. Stipules are sometimes present. The evolution of the *Rubiaceae* from Loganiaceous stock is imaginable and would involve but few structural changes. Sporne's work shows that both inferior and superior ovaries occur in primitive and very advanced families. There are even a few genera which are intermediate between the two families and many which have a similar facies. *Gaertnera* is often classed with the *Loganiaceae* because of its half-superior ovary but it is really a member of the *Psychotrieae*. Some *Canthium* spp. *(Vanguerieae)* are remarkably like *Strychnos* spp. *(Loganiaceae)*. Utzschneider holds that the many-ovuled ovary is the primitive condition in the

Rubiaceae but there is no evidence. Processes of reduction i.e. locules with numerous ovules giving rise to those with few ovules are more in keeping with the criteria of primitiveness put forward by Hutchinson et al. but this specific character is not mentioned by them. I believe that the *Rubiaceae* were evolved « on a broad front » and that two kinds of ovary were already represented as the family was emerging. Many *Loganiaceae* are aluminium accumulators and some contain raphide-like crystals.

The *Loganiaceae* and *Rubiaceae* had common ancestors, some of which had numerous ovules and some solitary ovules before the separation of the two families. The *Psychotrieae* group of tribes have diverged least and the *Hedyotideae* and finally *Rubieae* most as far as the *Rubioideae* are concerned. The separation into tribes was probably rapid and happened very soon after the family emerged. The *Knoxieae* indicate how the woody tribes of the *Rubioideae* may have given rise to herbaceous ones in dry places subjected to fires. Other herbaceous tribes could have been derived in connection with other special habitat conditions. In general, the *Guettardoideae* and *Cinchonoideae* have diverged less from the primitive stock. The *Ixoreae* group of tribes in the *Cinchonoideae* are the least divergent and compare with the *Psychotrieae* in this respect whereas the *Cinchoneae* are the most divergent. Certain facts such as the closeness in structure between the capsules of the *Cinchoneae* and *Hedyotideae*, the presence of bacterial nodules in some *Psychotria* and *Grumilea* and *Pavetta*, and the resemblances between many of the *Psychotrieae* and *Ixoreae* groups, may indicate definite cross relationships or mere convergence. It would serve no purpose to put these hypothetical ideas in the form of a chart.

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APPENDIX 1

Tables of the results of the examination of pollen, hairs, etc..., from certain genera representative of all the tribes.

For the purpose of these tables the classification of Hooker in Bentham and Hooker's « Genera Plantarum » has been followed since the material in very many large herbaria is so arranged.

Abbreviations used in the summary of results.

Hairs :	ext.	external.
	int.	internal.
	n-s.	non-septate.
	s.	completely septate, hairs made up of distinct cells.
	i-s.	incompletely septate i.e. there are a number of weak or strong partitions whithin the lumen of the hair but they do not cut the walls of the hair.
	tw.	thick-walled.
Pollen :	md.	minor diameter or width.
	mjd.	major diameter or width.
	colp.	colpate.
	equat.	equator, equatorial.

Notes on methods of preparation of hairs, pollen, etc.

Hairs.

These were examined in aqueous mounts under normal and polarised light.

Pollen.

Fresh anthers or boiled herbarium specimens were acetolysed with a mixture of 5 parts acetic anhydride and 1 part concentrated sulphuric acid. A few observations were made on material treated with acetic-sulphuric acid methods; the former method proved superior.

Testa cells.

When characters proved difficult to see, the use of 10 % sodium hydroxide proved satisfactory for clearing.

Raphides.

When abundant these can not be overlooked but in some cases the use of polarised light is of very great assistance.

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera.

Species	Hairs	Pollen	Remarks
Naucleeae.			
Adina microcephala (DEL.) HIERN.	Ext. n-s., tw., long and narrow. Int. flat, n-s., finely obliquely striated.	3-colp., pores large margined, extine pitted. ellipsoidal, md 17.6 μ.	
Uncaria africana G. DON.	Ext. i-s, tw., long and narrow. Int. nil.	3-colp., small, md 12.6 μ, grooves narrow, extine with fine unresolved sculpture.	
Mitragyna rubrostipulata (K. SCHUM.) HAV.	Ext. n-s. Int. n-s., sculpture slight.	3-colp., small, md 14.7 μ, grooves narrow but wider grooves containing them, bridged round pores. Extine moderately reticulate.	Testa cells with round pits in lumen.
Cinchoneae.			
Cinchona ledgeriana TRIM.	Ext. n-s., sculptured with oblong rugae. Int. n-s, closely muriculate with raised tubercles.	3-colp., md. 23.5 μ, pores moderate, extine finely granulated, faces between furrows with median ridges pronounced at poles.	Testa cells with borders of actual cells indistinct, inside with marked pits.
Crossopteryx febrifuga BENTH.	Ext. n-s., surface rugose. Int. nil.	3-colp. colpi short crossed by short equat. raised bands on either side of the pore, extine finely reticulate, md 17.6 μ.	Testa cells with walls tuberculate inside, lumina with small pits, dividing walls with thickenings between the pits, fingers of seed wings with small pits.
Hymenodictyon floribundum B. L. ROBINSON.	Ext. Int.,nil.	3-colp., md. 14.7 μ, reticulate.	Testa cells with anastomosing ridges which cut off irregular pits.

		very large open reticulation. Not like *Hymenodictyon* or *Crossopteryx*.	sculptured at all. Not at all like *Hymenodictyon* or *Crossopteryx*.
Condamineeae.			
Condaminea corymbosa Dc.	Ext. nil. Int. few, n-s., no sculpture.	3-colp., grooves rather wide, pores large, slight equatorial banding in pore area, md. 23.5 μ, reticulation moderately open and deep.	Testa cells with very faint reticulation and papillae, nothing which could be described as pits.
Chimarrhis turbinata Dc.	Ext. l-s., rugose. Int. n-s., with small rugulae.	3-colp., grooves narrow, extine thick, strongly reticulate, lumina small, grains ovoid, md. 20.5 μ.	Testa cells with an anastomosing network rather than pits.
Bikkia grandiflora Reinw. ex Blume.	Nil.	No grooves, angulaperturate, pores fairly large, 27.9 μ md.	
Portlandia albiflora Stand.	Nil.	3-colp., but grooves so shallow as to be merely marks, very wide with big pores. Grooves bridged in the pore area. Extine granular, md. 26.5 μ.	Crystal sand present — large granules in leaves. Testa after NaOH treatment shows deep pits in cell bottoms.
P. ghiesbreghtiana Baill.	Nil.	3-colp., grooves with ridges at either end and transversely elliptic pores, md. 20.6 μ.	
Pinckneya pubens Michx.	Ext. i-s., very curly, sculpture faint. Int. n-s., flat, with sculpture of small rugae diagonally arranged.	Elliptic, md. 23.5 μ, mjd. 26.5 μ, 3-colp. grooves narrow, constricted equatorially, reticulation deep but lumina not large.	Winged seeds, testa thin, cells with wide reticulation rather than pits.
Rondeletieae.			
Warszewiczia coccinea Klotzsch.	Ext. i-s., tw. Int. n-s., rugulose.	3-colp. extine thickish with open reticulation. Pores large margined, grooves bridged equatorially in the pore area, grains small, md. 16.1 μ.	Testa cells reticulate inside rather than pitted.

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Rondeletia trichotoma STAND.	Ext. i-s., tw., curly, no sculpture. Int. nil.	3-colp. extine thickish, with very fine reticulation, pores rather large, faint equat. band, grains small, 14.7 μ, grooves fairly wide.	Testa not successfully prepared.
R. pachyphylla KRUG. and URBAN.	Int. flat, striate, constricted very markedly at intervals, sides straight.	3-colp., grooves wide, bridged equat. in the pore area, extine finely reticulate, md. 16.1 μ.	
R. sp. (? *thyrsoidea*).	Ext. i-s., tw. Int. flat, n-s., but very constricted, constrictions elliptic, the planes of alternate ones at right angles.	3-colp., extine thin not sculptured.	
Wendlandia arabica DEFL.	Nil.	3-colp., grains ellipsoidal, reticulate.	Testa cells warted, vaguely reticulate.
Sickingia mexicana BULLOCK.	Ext. i-s., tw. Int. n-s., rugulose with raised granules.	3-colp., md. 30 μ, walls of grooves thin, pores moderate, reticulation uneven, lumina varying in size.	Excluded by Bremekamp. Flowers characteristic, truncate, open in bud? Testa cells with thick walls, lumina not pitted.
Deppea cornifolia BENTH.	Ext. i-s, tw. papillate. Int. nil.	3-colp., grooves narrow, pores rather small, no sculpture at all, md. 11.8 μ.	Flowers of open type, corolla lobes almost free to the base. Raphides present in corolla lobes, etc. Distinct pits in the testa cells. Excluded by Bremekamp.
Sipanea pratensis AUBL.	Ext. setiform, i-s., tw. Int. constricted, constrictions flat, ellipsoidal, finely striate.	3-colp., extine thickish, pitted (?), grooves small narrow, pores of moderate size, md. 32.3 μ.	No raphides, corolla very like *Otomeria*, foliage very similar to *Virectaria*, disc large annular, placentae

Pentas bussei KRAUSE.	Ext. s., minutely tuberculate or pitted. Int. flat, n-s., finely obliquely striate.	3-colp., furrows narrow, broad equat. band uninterrupted, extine finely reticulate or granular, md. 16.1 μ.	
P. ionolaena K. SCHUM.	Ditto.	3-4-colp., grooves narrow, faint equat. band, grains broadly ellipsoidal, extine reticulate, md. 21 μ.	
P. lanceolata (FORSK.) DEFLERS.	Ditto.	4-colp., grooves narrow, pores small, continuous broad equat. band, extine thick granular, md. 25 μ.	
P. schimperiana (A. RICH.) VATKE.	Ditto.	4-colp., grooves narrow, equat. band marked in region of pores, extine reticulate, md. 22.4 μ.	General for *Pentas*. Testa cells with somewhat wavy walls, minutely dotted lumina, under the true testa there seems to be a layer of thin-walled cells with pitted lumina or lumina with anastomosing ribs.
P. graniticola BRUCE.	Ditto.	3-colp., grooves narrow, pores small, grains broadly ellipsoidal, md. 44.1 μ, equat. band present in pore area, raised round pore, extine reticulate.	
P. decora SP. MOORE.	Ditto but ext. hairs small with few cells.	4-colp., grooves short, bridged in pore area, and each half of groove contained in middle of semi-elliptical broad area which is also bridged, pores moderate, edges raised, extine reticulate, md 38.2 μ.	
P. hindoioides K. SCHUM.	Ditto.	3-colp., grooves narrow. Interrupted equat. band surrounding pore area, extine finely reticulate, md. 35.3 μ.	

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Parapentas silvatica (K. SCHUM.) BREM.	Ext. s. Int. as in *Pentas*.	3-colp., reticulate.	
Sacosperma sp.	Ext. nil. Int. flat, n-s., longitudinally striate.		
Oldenlandia spp.	Ext. s. or n-s. Int. flat, striate, straight, or rarely very markedly constricted.		Bremekamp (1952) describes the pollen and testa cells of many of the species of this genus and its allies.
Pentodon pentander VTKE.	Ext. nil. Int. flat, striate, with interrupted longitudinal wavy lines, margins wavy.		
Dolichometra leucantha K. SCHUM.	Ext. short, conical but s. Int. n-s., thin-walled, rugulose faintly.	3-colp., grooves narrow, margined, short, extine finely reticulate, md. 41 μ.	Raphides present, testa cells with moderate walls and no pits.
Dirichletia pubescens KL.	Ext. long, s., with rugulae or no sculpture. Int. obliquely and somewhat irregularly striate.	4-colp., grooves narrow, extine closely reticulate, elliptic area around colpi thicker, banded round pores, md. 35.5 μ.	In young fruits only one erect ovule is visible, but often 4 in ovary locules. Testa cells oblong, walls moderate, not pitted. (N.B. *Placopoda virgata* BALF. F. also has only one seed per locule, testa cells thin not pitted.)
Otomeria oculata SP. MOORE.	Ext. s. long. Int. as in *Pentas*.	3-colp., grooves narrow, pores moderate, broad continuous equat. band. Extine thickish, reticulate.	
Virectaria major (K. SCHUM.) VERDC.	Ext. setiform, tw., i-s. Int. flat, thin-walled, no sculp-	3-colp., grooves long, moderate in breadth, constricted for	Removed from tribe by Bremekamp. Testa cells elon-

		bottom of groove with median deeper groove, pore small, extine very finely reticulate. Grains narrowly ellipsoidal, mjd. 35.3 μ.	lumina minutely warted. No raphides.
Ophiorrhiza spp. *(succirubra* KING, *mungos* L., etc.).	Ext. s., with longitudinal interrupted striae. Int. flat, n-s., interrupted striae.	3-colp., or angulaperturate, grooves short, usually wide and shallow, pores large, grains triangular in plan, md. 38.2 μ. Extine with very strong small reticulation, smallest in the area of grooves.	Removed from tribe by Bremekamp. Testa cells with thick walls which have marginal thinned areas like pits. Raphides in leaf vein tissues. Capsule very characteristic.
Spiradiclis caespitosa BL.	Nil.		Removed from tribe by Bremekamp. Testa cells with thick walls which are denticulate, lumina with small tubercles. Leaves contain optically active oblongs which separate into numerous needle-shaped crystals with difficulty, clearly raphides.
Bouvardia spp. (cultivated).	Ext. almost completely s., rugose. Int. nil, or flat, n-s., no sculpture.	3-colp., grooves narrow, pores small. Faint equat. banding in the pore area, extine with fairly strong reticulation.	Originally placed in the Cinchoneae. Raphides numerous, testa cells elongate, thin-walled no pits.
Mussaendeae.			
Mussaenda arcuata POIR.	Ext. long, i-s., tw. Int. flat, n-s., finely obliquely striate.	4-colp., grooves absent or short, wide and very shallow. Grains small, globose, somewhat square in section, md. 11.9 μ. Pores rather large, margined, sculpture faint, reticulate.	Testa cells with pits.

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Pseudomussaenda flava VERDCOURT.	As in *Mussaenda*.	3-colp.	Placed in the Condamineae by Wernham. Testa cells with many round pits in the lumina.
P. capsulifera (BALF. F.) WERNH.	Ext. i-s., tw. Int. flat, constricted, rugulose.	4-5-colp., grooves short, bridged by short equat. band in the area of the moderate pores. Extine finely reticulate, md. 26.5 μ.	Testa cells with large pits. The peculiar spathulate emarginate corolla lobes and other differences probably merit removal to a new genus.
Sabicea spp.	Ext. curly, n-s., or i-s, tw., no sculpture. Int. very markedly constricted, the constrictions often wider than long, particularly at the distal end of hair, often covered with warts. Other species have the constrictions longer with wider necks between them; n-s in each case.	3-4-porate, no grooves, extine reticulate. Grains oval, md. 26.5 μ.	Testa reticulate, difficult to see cell walls and tell difference between lumina and pits. General effect is a mass of elongate lumina with thick walls each lumen crossed by 4 ribs thus cutting off 5 pits.
Pauridiantha holstii (K. SCHUM.) BREM.	Ext. (leaf.) s. Int. flat, n-s., walls straight or undulate, with longitudinal interrupted striae.	3-colp., grooves rather wide, pore large. Extine with fine reticulation, md. 17.6 μ.	Placed in a separate tribe by Bremekamp. Optically active crystals resembling raphides are present.
Coccocypselum lanceolatum PERS.	Ext. i-s., tw. Int. n-s., flat, walls undulate, striate with wavy interrupted longitudinal marks.	3-colp., grooves short and narrow, crossed by short equat. ridge. Reticulation very fine, md. 23.5 μ.	Placed in a separate tribe by Bremekamp. Rod like crystals rather similar to raphides in leaf tissue and in *C. condalia* there are distinct clusters of needles. The plants show resemblance to *Hedyotideae* and herbaceous *Psychotrieae*. The fruits of

E. hypoleuca BENTH.	Int. flat, n-s., longitudinally striate.	large, elliptic, surrounded by a large raised elliptic area, characteristic. Extine with reticulate sculpture, the lumina of two sizes, md. 23.5 μ.	
Hamelieae.			(See text p. 248).
Hamelia patens JACQ.	Ext. long, s., cells long. Int. nil.	3-porate, angulaperturate.	Raphides present.
Bertiera montana HIERN.	Ext. i-s., tw., the septa are concave on both surfaces i.e. the lumina of the cells are rounded at each end. Int. n-s., walls constricted, undulate, longitudinally rugose.	3-colp., grooves narrow, md. 17.63 μ. Extine reticulate.	No raphides. Testa cells pitted.
Heinsia bussei VERDCOURT.	Ext. i-s., tw., septa inconspicuous and spaced. Int. flat, thin-walled, finely obliquely striate.	3-colp., grooves narrow, extine thin, reticulate, distorted by acetolysis, md. 14.7 μ.	No raphides. Testa cells with thick walls, lumina with marked pits.
Catesbaeeae.			
Catesbaea parvifolia DC.			No raphides, ovules warted. Testa thick, rugose.
C. spinosa L.	Ext. nil. Int. n-s., very fine, completely devoid of sculpture.	3-colp., grooves wide and long. Grains ovoid, lemon shaped, the poles protruding, grooves constricted equat. Extine with very fine ? granulation, not resolved.	Stamens long, free almost to the base.
Gardenieae.			No raphides in any.
Alibertia edulis A. RICH. and *A. elliptica* (CHAM.) SCHUM.	Ext. small, n-s., very thick walls. Int. n-s., flat, very rugose.	3-porate, angulaperturate, elliptic in lateral view, no grooves, md. 27.9 μ. Extine reticulate.	

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Posoqueria latifolia (RUDGE) ROEM. and SCHULT.	Nil.	3-porate, angulaperturate, reticulate.	Excluded from tribe by Bremekamp on pollination characters. Anthers with hard horny tips and bases, scaly hairs on the back.
Burchellia capensis R. BR.	Ext. i-s., tw., rugose. Int. thin, n-s., no sculpture at all.	3-porate, angulaperturate, reticulate.	
Leptactina benguelensis (WELW. ex BENTH. and HOOK. F.) GOOD.	Ext. peculiar bent n-s. trichomes, almost solid, lumen narrow, widening at bulbous base of hair. Int. n-s., flat, very rugulose.	4-colp., grains elliptic, md. 30 μ. Grooves moderate. Extine reticulate.	Other species have ext. hairs longer and i-s., but tw.
Macrosphyra longistyla (DC.) HOOK. F.	Ext. long or short, tw., i-s., or n-s. Int. n-s.	Pollen in tetrads, globose, reticulate.	
Rothmannia fischeri (K. SCHUM.) BULLOCK.	Nil.	3-colp., grooves moderate, pores small.	Testa cells thick-walled, small.
Didymosalpinx norae (SWYNN.) KEAY.	Ext. nil. Int. (style hairs) n-s., thin and very lightly sculptured.	3-colp., grooves narrow, pores moderate. Extine with wide reticulation, md. 26.5 μ.	
Gardenia jovis-tonantis (WELW.) HIERN.	Ditto.	Pollen in tetrahedral tetrads. No sculpture. Each grain with three pores so arranged that from any view of the tetrad with 3 grains facing one 3 pairs of pores are visible (others are visible at the back through the grains), pores margined.	Testa cells with boundaries indistinct, lumina with numerous pits with raised walls.
Porterandia penduliflora	Ext. i-s., tw.	3-porate, grooves represented by	

		by reticulate band. Extine openly reticulate, muri with rods, md. 32.5 μ.	
Oxyanthus speciosus Dc.	Ext. nil. Int. thin, n-s., no sculpture.	Pollen in tetrahedral tetrads.	Testa cells elongate, walls thick, internal margins nodulose, no lumen sculpture.
Galiniera coffeoides Del.	Nil.	3-colp., md. 26.5 μ, extine reticulate.	Probably referable to *Ixoreae*. Testa cells thick-walled, no pits.
Ixoreae.			Many of these genera transferred from the *Gardenieae* (Bremekamp, 1934).
Tarenna graveolens (Sp. Moore) Brem.	Ext. nil. Int. flat, n-s., with oblique interrupted striae.	3-colp., grooves narrow, pores small bordered, crossed by transverse bridge, actually a thinning of the rather thick extine, md. 20.5 μ.	Testa cells roundish, walls thin, with rounded or rectangular thickenings, no lumen sculpture.
Enterospermum littorale Hiern.	Ext. nil. Int. long, flat, n-s., with longitudinal rugae.	3-colp., grooves very shallow, extine finely reticulate, md. 17.6 μ.	Testa cells thin, lumen with scattered yellow dots.
Feretia apodanthera Del.	Ext. n-s., no sculpture. Int. n-s., slight sculpture.	3-colp., md. 23.5 μ (or 17.6 μ in some) grooves narrow, thin, extine with fine unresolvable sculpture.	Testa cells thin with no sculpture.
Kraussia kirkii (Hook. f.) Bullock.	Ext. nil. Int. long, n-s., faint sculpture of rugae.	3-colp., grooves short and narrow, with wide bridge containing the moderate pores.	Testa cells round, thick-walled, sculpture obscure.
Morelia sp.	Ext. nil. Int. n-s., thin, flat, no sculpture.	3-porate, pores with annulus, extine thick, reticulate, md. 20.6 μ.	
Rutidea syringoides (Webb) Brem.	Ext. i-s., tw., no sculpture, or in leaf n-s. Int. n-s., flat rugose.	3-4-colp. grooves very narrow. Extine finely reticulate, md. 16.2 μ.	Testa cells thin, no sculpture.

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Ixora sp.	Ext. thin, n-s., papilla hairs. Int. nil.	3-colp., extine thick, grooves and pores moderate in size, md. 20.5 μ.	
Tricalysia sp.	Ext. long, i-s., mod. tw. Int. long, flat, sculpture very fine.	3-colp., grooves moderate, pores large in a diamond-shaped bridge, extine finely reticulate, md. 24 μ.	Testa cells thin, hexagonal, each containing a large circular air bubble when mounted.
Coffea sp.	Nil.	3-colp. or 3-porate, grooves very vague. Extine with very fine reticulation, md. 26.5 μ.	Testa cells long, cigar-shaped, tw., walls with channels; or circular like pits in a matrix with no sculpture.
Pavetta silvicola BREM.	Ext. n-s., tw., rugose. Int. n-s., long, flat, thin-walled, sculpture faint.	3-colp., grooves fairly wide, diamond-shaped, equat. area raised round pore. Extine finely reticulate.	Testa cells thin with no sculpture.
Cruckshanksieae.			
Cruckshanksia hymenodon HOOK. et ARN.	Ext. minute raised papillae from the cells of foliaceous calyx lobe and leaf hairs, etc., small thin finely granular. Int. nil.	3-colp., grooves long, pores moderate, reticulation very wide, md. 45 μ or less.	Raphides present. Flowers heterostylous.
Retiniphylleae.			
Retiniphyllum schomburgkii MÜLL. ARG.	Ext. n-s., no sculpture. Int. thin, n-s., no sculpture.	3-colp., grooves rather narrow, with raised equat. bridge in pore area, sides of bridge sloping towards groove, pores large. Extine with very large open reticulation. Grains ellip-	Gardenioid appearance; anthers with basal appendage. No raphides.

Guettarda speciosa L.	Ext. wiry, n-s. Int. fine-walled, n-s., rounded tips, no sculpture.	3-4-porate, pores large with conspicuous thickened annulus, the outer margin of which is crenulated. Extine faintly granular. Grains angulaperturate rounded-triangular or square in plan, md 38.2 μ.	No raphides. Testa cells with thin walls, lumina with very characteristic structure of irregularly shaped pits, some of which are open i.e. not completely bounded by a thick wall but by the thin cell wall.
Timonius confertiflorus MERR.	Ext. *i-s.*, tw. Int. hairs at back of stamens are similar and *i-s.* (checked many times).	3-porate, pores moderate not bordered. Extine with a very wide reticulation, the rods of the muri are plainly visible and the lumina 5-6 μ in width, md. 32.3 μ.	Testa cells rectangular, thick-walled with no sculpture.
T. wallichianus VALETON.		Pollen similar to above, pores smaller with two « guard cells ». Muri of the very wide reticulation raised, rods not evident, md. 22 μ.	
Knoxieae.			
Pentanisia ouranogyne SP. MOORE.	Ext. s. Int. thin-walled, long, fine close striae, oblique.	3-colp., grooves moderate, pores rectangular, the grooves are short and not visible in polar view. Extine with very wide reticulation, muri with patches (rods ?). Lumina 1.5 μ, md. 23.5 μ.	Raphides present. Testa cells thin with no sculpture.
Knoxia corymbosa WILLD.	Ext. s., roughened. Int. thin, flat, with sculpture of oblique fine striae.	3-colp., grooves almost linear. Pores narrow. Extine thick, with rather close but strong reticulation, rods in muri conspicuous, md. 30 μ.	Raphides present.

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Chiococceae.			
Chiococca alba (L.) HITCH.	Ext. nil. Int. small, thin-walled, no sculpture.	3-colp., grooves narrow, extine very finely granular. Grains narrowly ellipsoidal, md. 17.6 μ.	Leaves and fruit resemble Vanguerieae, particularly *Canthium*. No raphides. Testa with thin-walled sculptureless cells, or? with very faint pits (later observation).
Alberteae.			
Alberta magna E. MEY.	Ext. n-s., no sculpture. Int. n-s., tw., no sculpture.	3-colp., grooves moderate bridged on either side of the rather large pores. Extine finely reticulate, md. 29 μ.	No raphides.
Heinsenia diervilleoides K. SCHUM.	Nil.	3-colp., grooves moderate, extine reticulate, md. 21 μ.	No successful testa preparation prepared.
Lamprothamnus zanguebaricus HIERN.	Ext. nil. Int. n-s., smooth or ridged.	3-colp., grooves with diamond-shaped bridge around the margined pores. Extine finely reticulate, md. 25 μ.	See text p. 248 for correct position of these last two genera.
Polysphaeria parvifolia HIERN.	Ext. i-s., striate. Int. n-s., sculptured with longitudinal rugae.	3-colp., extine reticulate, grooves rather narrow, surrounded by an elliptic area of thicker extine, bridged by very thin area, pores large, md. 29.4 μ.	Testa cells brown, irregular and ill-defined.
Cremaspora triflora (THONN.) K. SCHUM.	Ext. tw., i-s., or n-s. Int. thin-walled, n-s., sculpture faint.	3-colp., grooves narrow, long, constricted for middle third. Extine finely reticulate, md.	

Canthium hispidum BENTH.	Ext. tw., i-s. Int. n-s., thin, margins straight or wavy, no sculpture.	3-porate, angulaperturate, pores large, elliptic. Extine reticulate rather closely. Grains ellipsoidal in equat. view, md. 32.5 μ.	No raphides in any of the genera. Style capitate, in all the pollen is 3-porate and when viewed before acetolysis drops are exuding from the large pores. Testa cells hexagonal with no sculpture.
Rytigynia amaniensis (KRAUSE) BULLOCK	Ext. ditto. Int. ditto, straight margins.	Similar.	
Fadogia sp.	Ditto.	Similar.	
Temnocalyx sp.	Ditto.	Similar.	
Tapiphyllum sp.	Ditto.	Similar.	
Robynsia sp.	Ditto.	Similar.	
Lagynias spp.	Ditto.	Similar.	
Cuviera spp.	Ditto.	Similar.	
Vangueria spp.	Ditto but int. with faint longitudinal sculpture.	Similar, 3-porate, no grooves or sculpture, grains, 38.2 μ, pores 10.3 μ.	Testa cells with slightly undulate thin walls, lumen oily, with fine ridges and traces of pits.
Craterispermum laurinum BENTH.	Ext. nil. Int. n-s., margins crinkled rugulose.	3-porate, pores small, margined. Extine thick, strongly reticulate. Grain broadly ellipsoidal, circular in polar view, md. 26.5 μ.	Differs from other members of the tribe very markedly. Stigma bifid; shows heterostyly. There are rod-like crystals very like true raphides in the leaves. (See text p. 240).
Ixoreae. (See after *Gardenieae*.)			

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Morindeae.			
Morinda asteroscepa K. SCHUM.	Ext. papillae only, n-s., tw. Int. exceedingly characteristic, n-s., with spirally twisted frill from top to bottom.	3-porate, angulaperturate, pores fairly small, extine granulate, md. 47 μ.	Raphides very abundant in fruit. Testa cells oblong or rounded, with true small pits in horny yellow lumen.
Prismatomeris labordei MERR.			Rodlike crystals rather than true raphides.
P. tetrandra K. SCHUM.	Nil.	3-colp., grooves very narrow, straight, pores narrow. Extine with moderately large reticulation, muri fine and little raised, md. 29.4 μ.	Fruits « Psychotrioid ».
Coussareeae.			
Coussarea congestiflora MÜLL. ARG. *C. cornifolia* BENTH. and HOOK. F.	Nil.	2-porate, pores very large. Grains highly characteristic like cylinders open at both ends. Annulus around the pores i.e. ends of thickened tissue. Sides of cylinders convex. Extine granulate, more so in annular areas, length 29.4 μ, md. 20.6 μ.	Rodlike crystals present and true raphides abundant in the fruit tissues. Fruit one-locular , pericarp fibrous. Testa cells irregularly quadrangular, walls thin but with subspherical markings at intervals.
Faramea spp.		3-porate.	See remarks on the pollen by Erdtman (1952).
Psychotrieae.			
Psychotria kirkii HIERN.	Ext. s. Int. n-s., margins wavy, sculpture of wavy lines	3-porate, angulaperturate, extine thick, dark brown, very reticulate lumina 2.3 μ wide grains	Raphides present in all, usually abundant. In other species of the genus the

			corns ». Testa cells rounded or quadrangular, walls rather thick, no pits.
Grumilea spp.	Ext. long, s. Int. n-s., thin-walled, rugose or striate.	Similar but, md. 55.9 μ.	
Chasallia albiflora KRAUSE.	Similar when present.	4-porate, pores large, elliptic like short grooves, extine rather widely reticulate, md. 59 μ.	
Camptopus goetzei (K. SCHUM.) KRAUSE.	Ext. long s.		
Geophila hirsuta BENTH.	Ext. very long, s. Int. n-s.	Pores not visible, extine strongly warted, spherical, md. 53 μ.	Fruit like *Pentanisia,* testa cells thin, no sculpture.
Lasianthus kilimandscharicus K. SCHUM.	Ext. s. or n-s. Int. n-s., margins wavy, sculpture of wavy lines.	3-4-porate, angulaperturate, pores largish, lipped, extine thick, strongly reticulate, md. 41 μ.	Raphides confined to the fruits in this species.
Triainolepis hildebrandtii VTKE.	Ext. i-s., small and rugulose, on corolla, s. Int. n-s., sculptured with distant oblique lines.	3-colp., grooves narrow, grains with broad raised equat. band and interrupted parallel areas above and below it so that at certain angles crosses can be seen on the faces, extine finely reticulate, md. 26.5 μ.	Calyx lobes a little unequal. Raphides very abundant, disc present, ext. hairs are intermediate between s. and i-s.
Paederieae.			
Paederia foetens (HIERN) K. SCHUM.	Ext. s. Int. n-s., cylindric or clavate, sculptured with oblique rugulae.	3-colp., grooves moderate, extine thick, warted (large warts).	Raphides present. Corolla tube splits at base and filaments are free basally as in some *Pentas*. Testa cells thin with no sculpture, but packed with raphides.

Summary of results of the examination of pollen, hairs, etc. of various Rubiaceous genera *(continued)*.

Species	Hairs	Pollen	Remarks
Anthospermeae.			
Anthospermum herbaceum L. F.	Ext. s., or n-s., short. Int. nil.	3-colp., grooves broad, extine thick, finely granular. Grains markedly fossaperturate, md. 23.5 μ.	Raphides present in all genera. Testa cells with thickish walls, no sculpture.
Otiophora pycnostachys K. SCHUM.	Ext. s. Int. s., roughened, striate (base of stamens).	3-colp., grooves moderate, extine thick, warted, thin in bridge containing pore, md. 35.4 μ.	
Coprosma longifolia GRAY.	Ext. nil. Int. nil.	3-colp., grooves moderate, pores transversely elliptic, no noticeable sculpture. Grains subspherical somewhat triangular in polar view, md. 26.5 μ.	♀ form long styles, almost separate, stigmatic papillae prominent. ♂ form stamens free.
Spermacoceae.			
Borreria dibrachiata (OLIV.) K. SCHUM.	Ext. n-s., roughened. Int. nil.	Grains large, disc-shaped, 73.5 μ in diam. and 20.6 μ thick, approx. 21-colp. grooves short covering only the thicker outer part of the disc, 10 μ long. Extine finely reticulate and with scattered warts.	Raphides in all the genera. N. B. Other species of the genus e.g. *B. ruelliae* K. SCHUM. have septate external hairs.
Diodia spp.	Ext. s. or n-s.	Similar to *Borreria*.	
Richardia scabra L.	Ext. s. Int. thin, margins wavy, no sculpture.	Similar to *Borreria* but 18-colp., and less finely reticulate.	
Hypodematium sphaerostigma A. RICH.	Ext. s. Int. n-s., thin-walled, no sculp-	Similar, 12-colp., grooves very shallow, extine reticulate, md.	Probably synonymous with the genus *Staelia*.

Mitrocarpum verticillatum VTKE.	Ext. short, n-s. Int. short, n-s., blunt, wavy margins, ridged.	6-colp., grooves long, spreading the length of the subspherical grains, extine reticulate, md. 23.3 μ.	
Rubieae (Galieae).			
Galium stenophyllum BAKER.	Ext. n-s., short. Int. nil.	9-colp., grooves long, very narrow, spreading over the body of the ellipsoidal grains but not over the rounded and rather protuberant polar areas, extine sculpture very fine, not resolved, md. 18 μ. Other species are 7-8 colp.	Raphides present, stems square. Testa cells thin, no sculpture.
Rubia cordifolia L.	Ext. n-s., or i-s. Int. nil.	6-colp. similar to *Galium*.	
Loganiaceae. (A few selected ones are included here.)			
Gaertnera spp. (often included in the tribe *Psychotrieae* of the *Rubiaceae* from which they differ *only* in the superior ovary).	Ext. nil. Int. n-s., margins wavy, finely striate with longitudinally interrupted striae.	3-colp., grooves broad, sculpture very fine not reticulate, md. 32.3 μ.	
Strychnos spp.	Ext. various. Int. n-s., margins very wavy, sculpture of longitudinally interrupted striae.	3-colp., grooves broad, no sculpture, grains ellipsoidal, md. 20.6 μ.	

APPENDIX 2.

Bremekamp's latest views since the main part of my paper was written may be summarised as follows. (Bremekamp *in litt.*).

The *Rubiaceae* are divided into six subfamilies :

Cinchonoideae, Urophylloideae (one tribe *Urophylleae*), *Ophiorrhizoideae, Guettardoideae* (one tribe *Guettardeae*), *Ixoroideae* and *Rubioideae*. These subfamilies contain the following tribes.

Cinchonoideae : Cinchoneae, Naucleeae, Condamineeae, Rondeletieae, Sipaneeae, Manettieae, Mussaendeae, Sabiceeae.

Ophiorrhizoideae : Ophiorrhizeae, Pomazoteae.

Ixoroideae : Coptosapelteae, Cremasporeae, Gardenieae, Ixoreae, Vanguerieae.

Rubioideae : Hedyotideae, Argostemmateae, Coccocypseleae, Schradereae, Spermacoceae, Anthospermeae, Rubieae, Psychotrieae, Gaertnereae, Coussareeae, Morindeae, Paederieae, Knoxieae, Hamelieae, Hillieae, Triainolepideae (°).

Only the last tribe mentioned has been validly published (Proc. Kon. Nederl. Akad. v. Wetenschappen Ser. C., LIX, p. 3 (1956). I do not agree with this number of tribes as will be seen from the main part of my text. Twelve taxa which I accept need validating and at least some of these should be attributed to Bremekamp although some of the names which I have used and which he also uses e.g. *Cinchonoideae* cover widely different concepts. They could however be cited as (Bremekamp ex) Verdcourt emend. The types of the groups are of course those genera from which the names are derived. The content of the groups can be seen from my synopsis of classification given in the text.

Cinchonoideae (subfamilia *Rubiacearum*) :

> *Arbores, frutices* vel rarissime *herbae*, indumento e pilis non valvulatis composito vestiti, raphium fasciculis numquam instructi; stipulae saepe integrae. *Flores* numquam perfecte heterostyli; corollae lobi valvati, imbricati vel contorti; stylus divisus vel capitatus; ovula in loculis ± numerosa vel solitaria. *Fructus* siccus vel carnosus, dehiscens vel indehiscens; semina albuminosa; cellulae testa basi saepe conspicue perforatae.

Guettardoideae (subfamilia *Rubiacearum*) :

> *Arbores* vel *fructives*, indumento e pilis non perfecte valvulatis composito vestiti, raphium fasciculis numquam instructi. *Flores* non heterostyli; corollae lobi imbricati vel valvati; ovula solitaria pendula. *Fructus* 2-∞-pyrena vel putamine 2-∞-loculari, rarius dicoccus; semina ± exalbuminosa; cellulae testa basi haud sculpturatae.

Rubioideae (subfamilia *Rubiacearum*) :

> *Herbae, frutices* vel rarius *arbores*, saepe indumento e pilis valvulatis composito vestiti, raphium fasciculis ± dense instructi; stipulae saepissime fimbriatae. *Flores* saepe perfecte heterostyli; corollae lobi valvati, rarissime imbricati vel contorti (*Hamelia, Deppea* et *Hillia*); stylus saepe bilobatus, lobis linearibus instructis; ovula in loculis ± numerosa vel solitaria. *Fructus* siccus vel carnosus, dehiscens vel indehiscens; semina albuminosa; cellulae testae basi saepe punctatae sed non (vel rarissime) perforatae.

(°) In *Bull. Jard. Bot. État Brux.*, XXVII, p. 159-166 (1957), Bremekamp erects and discusses a new tribe, *Lathraeocarpeae*.

Schradereae (tribus *Rubioidearum*) :

Fructices epiphytici. Flores coreacei in capitulum globosum bracteatum dispositi; ovarium 2-4-loculare, ovulis numerosis. *Fructus* carnosus.

Urophylleae (tribus *Rubioidearum*) :

Frutices, arbores vel rarius *herbae. Ovarium* 2-∞-loculare, ovulis numerosis; granula pollinis 3-colporata; colpae cum pori germinali magni. *Fructus* baccatus.

Craterospermeae (tribus *Rubioidearum*) :

Frutices vel *arbores* parvae, raphium fasciculis ± sparse instructi. *Flores* heterostyli; ovarium 2-loculare; ovula solitaria pendula; granula pollinis porata. *Fructus* baccatus.

Argostemmateae (tribus *Rubioidearum*) :

Herbae fragiles. *Corolla* rotata, valde divisa; ovarium 2-loculare, ovulis numerosis; antherae conniventes, saepissime poris terminalibus dehiscentes. *Capsula* apice dehiscens.

Ophiorrhizeae (tribus *Rubioidearum*) :

Herbae. Ovarium 2-loculare, ovulis numerosis; discus carnosus. *Capsula* late obcordata, loculicide dehiscens.

Condamineinae (subtribus *Condamineearum*) :

Defined as for *Condamineeae* in Gen. Pl.

Rondeletiinae (subtribus *Condamineearum*) :

Defined as for *Rondeletieae* in Gen. Pl.

Cremasporinae (subtribus *Ixorearum*) :

Arbores vel *frutices. Corollae* lobi contorti; ovarium 2-loculare; ovula in loculis solitaria, ab apice fere pendula; radicula supera.

Heinseniinae (subtribus *Ixorearum*) :

Arbores vel *frutices;* maxime ut *Ixorinae,* corolla campanulata differt.

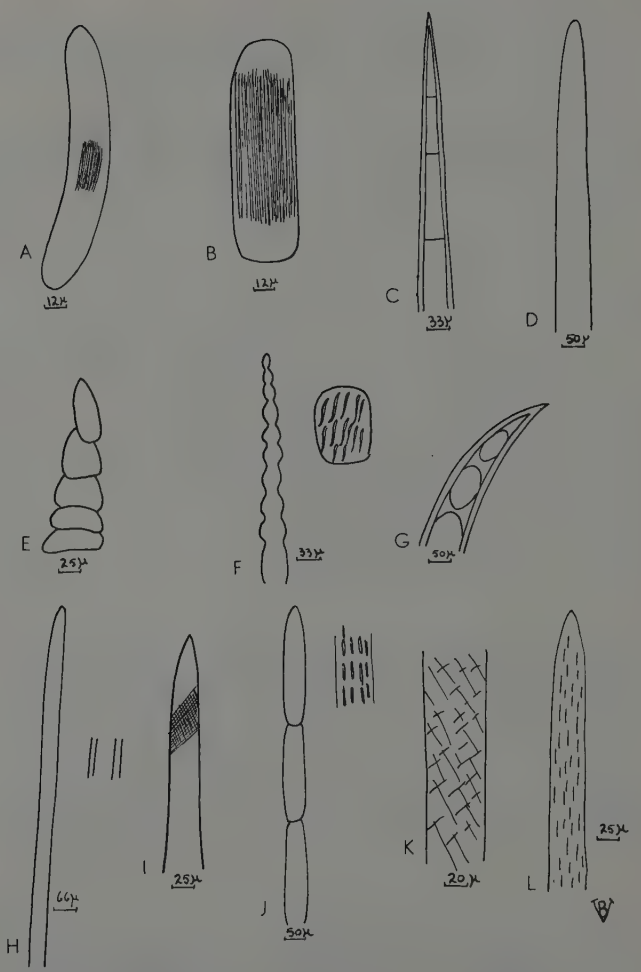
Heinsiinae (subtribus *Mussaendearum*) :

Arbores vel *frutices;* maxime ut *Mussaendinae, corollae* lobis imbricatis differt.

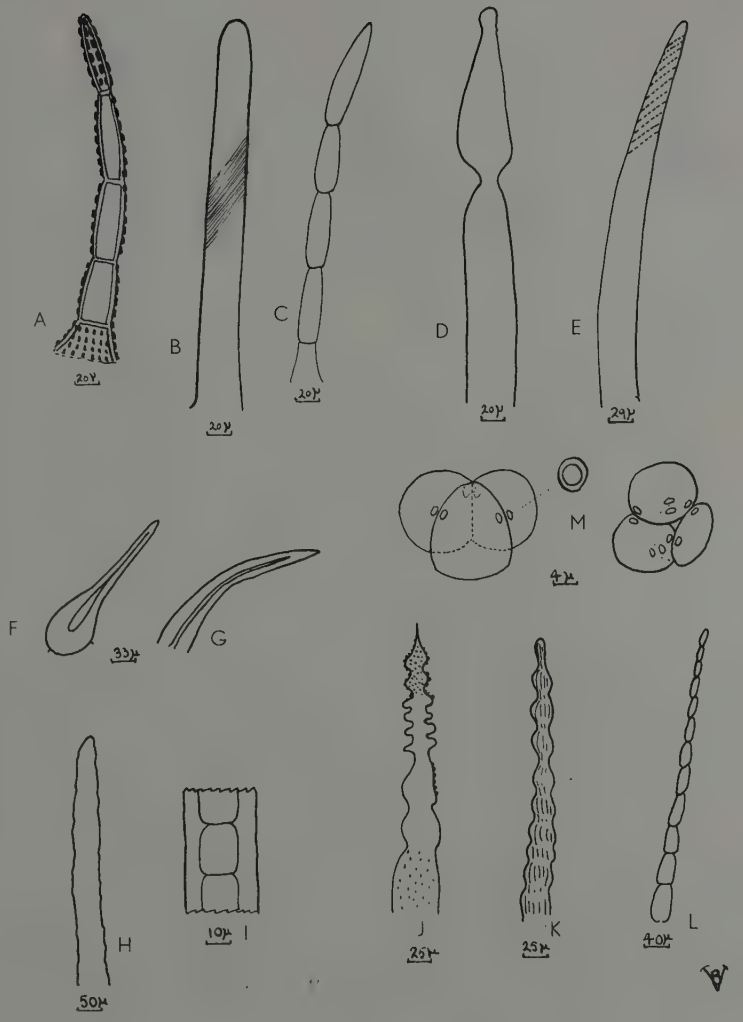
ADDENDA.

1) The generic name *Hypodematium* A. Rich. is preoccupied. Tennant (*Kew Bull.,* 1957, p. 386 (1958) has proposed the new name *Arbulocarpus.* It could probably, however, be accomodated in the genus *Staelia* Cham. & Schlecht.

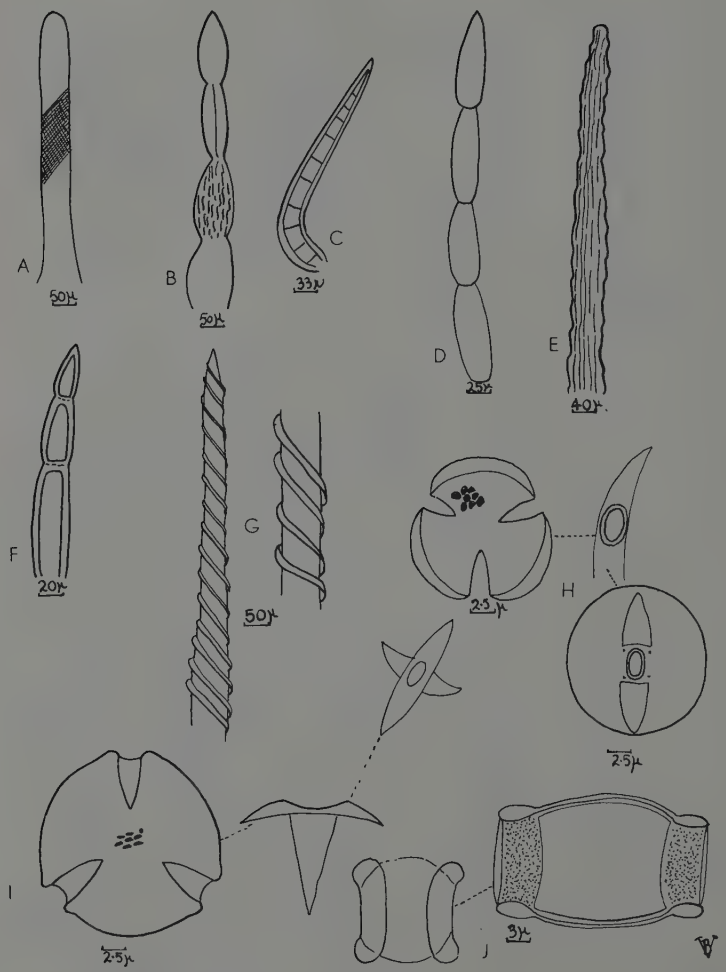
2) I overlooked the fact that Spencer Moore had already discussed the genus *Heinsenia* K. Schum. (*J. Linn. Soc., Bot.,* XL, p. 85-87 (1911). He found that there were two ovules in each loculus, buried in the placenta and removed the genus from the *Alberteae* to the *Gardenieae* where he placed it next to *Empogona* i.e. he is in general agreement with my independent placing.



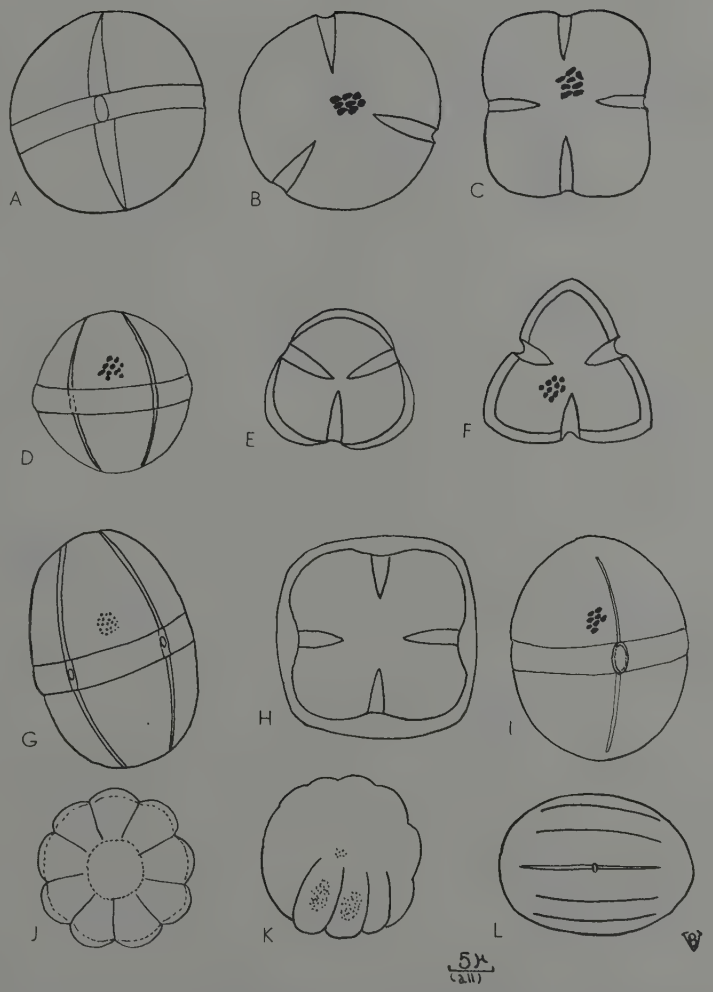
A, raphides, *Pentas lanceolata* (FORSK.) DEFLERS, subsp *quartiniana* (A. RICH.) VERD.; B, raphides, *Triainolepis hildebrandtii* VTKE; C, leaf hair, *Virectaria major* (K. SCHUM.) VERD.; D, hair from inside of corolla, ditto; E, leaf hair, *Dolichometra leucantha* K. SCHUM.; F, hair from inside of corolla, *Bertiera montana* HIERN; G, hair from outside of corolla, ditto; H, hair from outside of corolla, *Adina microcephala* HIERN; I, hair from inside of corolla, ditto; J, hair from outside of corolla, *Dirichletia pubescens* KLOTZSCH; K, hair from inside of corolla, ditto; L, hair from inside of corolla, *Oldenlandia herbacea* (L.) ROXB.



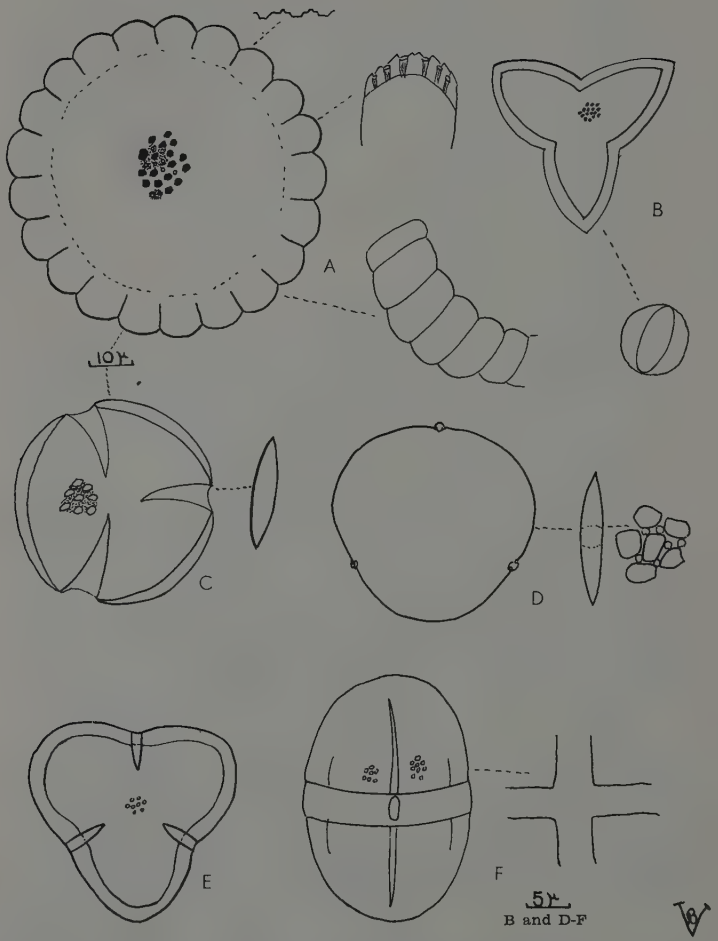
A, leaf hair, *Pentas bussei* KRAUSE; B, hair from inside of corolla tube, *P. lanceolata* (FORSK.) DEFLERS; C, hair from outside of corolla tube, ditto; D, hair from inside of corolla tube, *Guettarda speciosa* L.; E, hair from inside of corolla tube, *Tarenna graveolens* BREM.; F, hair from corolla lobes, *Leptactina heinsioides* HIERN; G, ditto; H, hair from inside corolla, *Canthium hispidum* BENTH; I, portion of leaf hair, *Canthium hispidum* BENTH; J, hair from inside of corolla, *Sabicea* sp.; K, hair from inside of corolla, *Lasianthus kilimandscharicus* K. SCHUM.; L, leaf hair, *Geophila hirsuta* BENTH.; M, pollen, *Gardenia jovis-tonantis* (WELW.) HIERN.



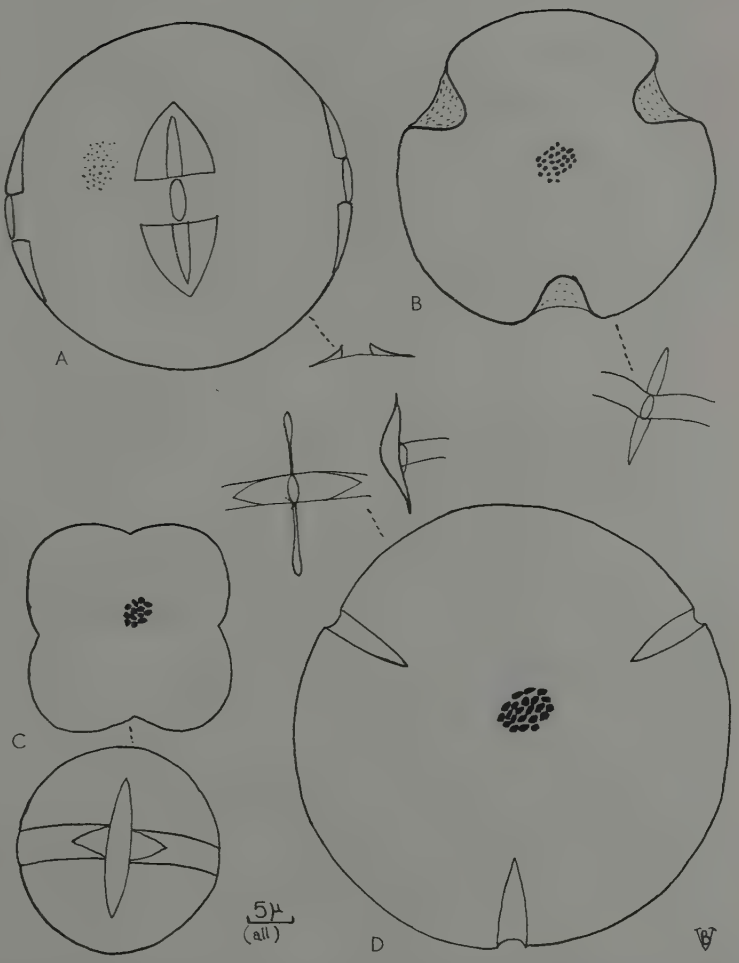
A, hair from inside of corolla, *Pentanisia ouranogyne* SP. MOORE; B, hair from inside of corolla, *Rondeletia* sp.; C, hair from outside of corolla, ditto; D, hair from bract, *Camptopus goetzei* (K. SCHUM.) KRAUSE; E, hair from inside of corolla, *Psychotria kirki* HIERN; F, hair from outside of corolla, *Triainolepis africana* HK. F.; G, hair from inside of corolla, *Morinda asteroscepa* K. SCHUM.; H, pollen, *Warszewiczia coccinea* (VAHL) KLOTZSCH; I, pollen, *Pavetta silvicola* BREM; J, pollen, *Coussarea cornifolia* BENTH. & HOOK.



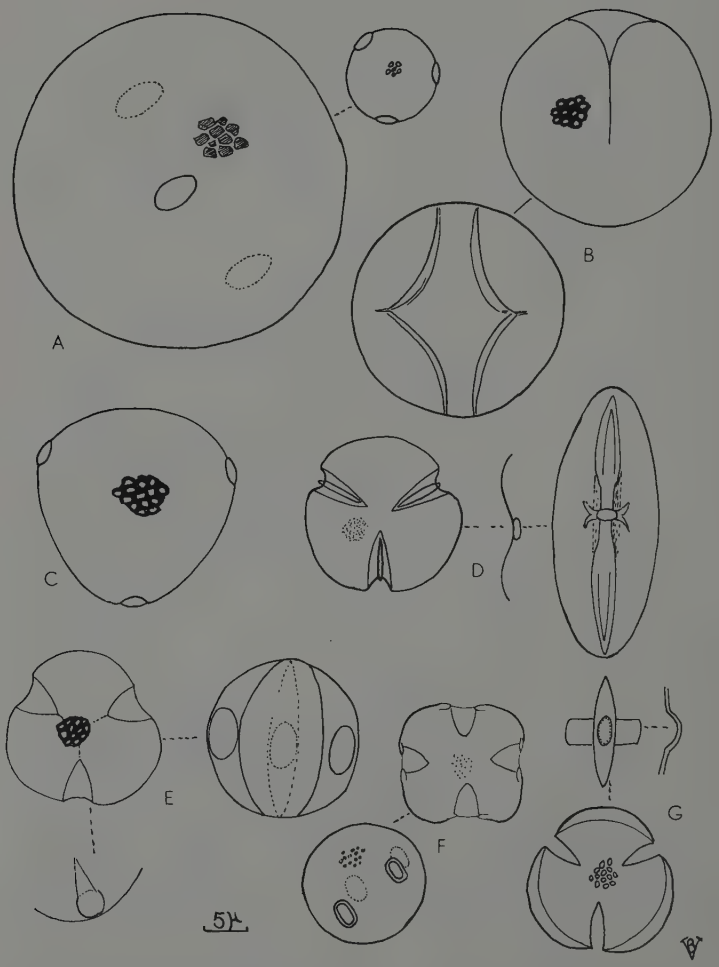
A, B, C, pollen, *Pentas ionolaena* K. SCHUM; D, E, pollen, *P. bussei* KRAUSE; F, I, pollen, *Otomeria oculata* SP. MOORE; G, H, pollen, *Pentas lanceolata* (FORSK.) DEFLERS; J, K, L, pollen, *Galium stenophyllum* BAKER.



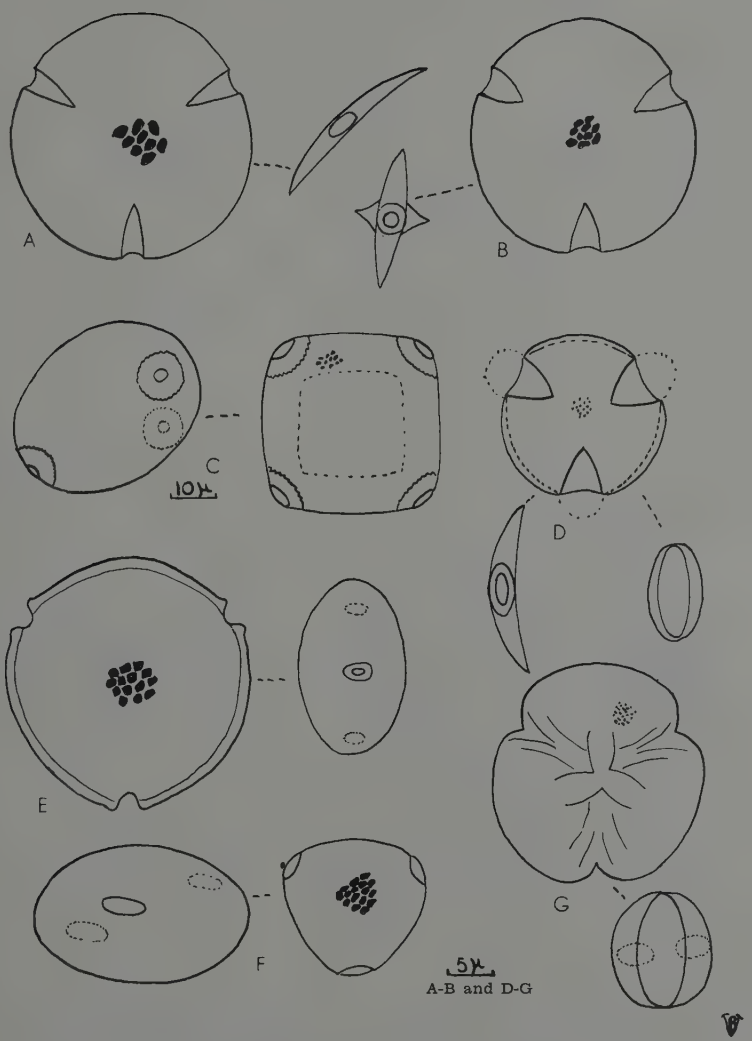
A, pollen, *Borreria dibrachiata* (OLIV.) K. SCHUM.; B, pollen, *Anthospermum herbaceum* L. F.; C, pollen, *Paederia foetens* (HIERN) K. SCHUM.; D, pollen, *Pentanisia ouranogyne* SP. MOORE; E, F, pollen, *Triainolepis hildebrandtii* VTKE.



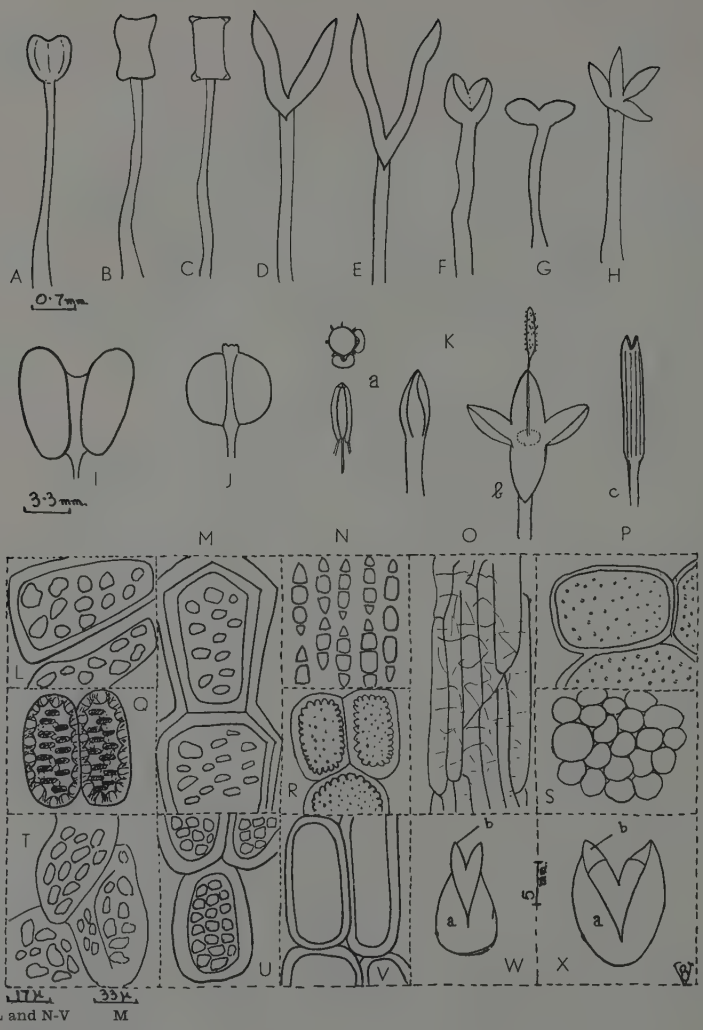
A, pollen, *Pentas decora* SP. MOORE emend.; B, pollen, *P. hindoioides* K. SCHUM.; C, pollen, *P. schimperiana* (A. RICH.) VTKE; D, pollen, *P. graniticola* BRUCE.



A, pollen, *Psychotria kirkii* HIERN; B, pollen, *Bouvardia* garden hybrid; C, pollen, *Morinda asteroscepa* K. SCHUM.; D, pollen, *Virectaria major* (K. SCHUM.) VERD.; E, pollen, *Pauridiantha holstii* (K. SCHUM.) BREM.; F, pollen, *Mussaenda arcuata* POIR.; G, pollen, *Crossopteryx febrifuga* (AFZEL. ex DON) BENTH.



A, pollen, *Didymosalpinx norae* (SWYNN.) KEAY; B, pollen, *Lamprothamnus zanguebaricus* HIERN; C, pollen, *Guettarda speciosa* L.; L, pollen, *Adina microcephala* HIERN; E, pollen, *Craterispermum laurinum* BENTH.; F, pollen, *Canthium schimperianum* A. RICH.; G, pollen, *Cinchona ledgeriana* (HOW.) MOENS ex TRIM.



A, stigma of *Rytigynia* sp.; B, ditto, *Vangueria rotundata* ROBYNS; C, ditto, *Canthium gueinzii* SOND.; D, ditto, *Craterispermum laurinum* BENTH.; E, ditto, *Pentas lanceolata* (FORSK.) DEFLERS; F, ditto, *Pauridiantha holstii* (K. SCHUM.) BREM.; G, ditto, *Psychotria abrupta* HIERN; H, ditto, *Lasianthus* sp.; I, fruit, *Canthium mundtianum* CHAM. et SCHL.; J, fruit, *Chiococca alba* (L.) HITCH.; K, pollen mechanism in *Pavetta elliotii* K. SCHUM., *a)* anthers adhering to stigma in unopened bud, *b)* opened flower and *c)* stigma with true stigmatic surface opened; L, testa of *Pseudomussaenda flava* VERD.; M, ditto, *Heinsia crinita* (AFZEL.) G. TAYLOR; N, ditto, *Sabicea* sp.; O, ditto, *Bouvardia laevis* MART.; P, ditto, *Pentas lanceolata* (FORSK.) DEFLERS; Q, ditto, *Crossopteryx febrifuga* BENTH.; R, ditto, *Spiradiclis caespitosa* BLUME; S, ditto, *Pentanisia schweinfurthii* HIERN; T, ditto, *Cinchona ledgeriana* MOENS ex TRIM.; U, ditto, *Bertiera bracteolata* HIERN; V, ditto, *Schismatoclada trichopharynx* BAKER; W, half of mature capsule with all calyx tissues removed, *Pentas nobilis* SP. MOORE, *a)* is interface between cocci and *b)* is beak; X, ditto, *Hindsia* sp.

NOTES ON *RUBIACEAE* FOR THE « FLORA OF WEST TROPICAL AFRICA » — II

BY

R. W. J. KEAY.

TRICALYSIA A. Rich. ex DC.

Tricalysia Talbotii (Wernham) Keay, comb. nov.

Cremaspora Talbotii Wernham, Cat. Talb. Nig. Pl., p. 49 (1913); Hutch. et Dalz., Fl. W. Trop. Afr. II, 1, p. 85 (1931).

Type : E. Nigeria, Oban, *Talbot* 287 (BM, holotype ! K, isotype !).

Observations. — 1. — This species, which has 2 ovules on each placenta and divergent style-arms, clearly belongs to *Tricalysia* and not to *Cremaspora*.

2. — It is closely allied to *T. Deightonii* Brenan and *T. gabonica* Hiern.

Tricalysia Wernhamiana (Hutch. et Dalz.) Keay, comb. nov.

Cremaspora Wernhamiana Hutch. et Dalz., Fl. W. Trop. Afr. II, 1, p. 85 (1931).
Coffea Talbotii Wernham, Cat. Talb. Nig. Pl., p. 52 (1913).

Type : E. Nigeria, Oban, *Talbot* 1620 (BM, holotype ! K, isotype !).

Observations. — 1. — This species is so far only known from the type gathering.

2. — It is a species in which there is only one ovule in each cell of the ovary. The relatively large ellipsoid placentas are peltately attached to the septum back to back, and on the outer side of each placenta a single ovule is borne in a depression. Such an arrangement does not occur in typical *Coffea* species so far as I know.

3. — The style has two divergent arms; a character which should have excluded this species from *Cremaspora*.

Tricalysia okelensis HIERN var. **oblanceolata** (HUTCH. et DALZ.) KEAY, stat. et comb. nov.

Tricalysia oblanceolata HUTCH. et DALZ., Fl. W. Trop. Afr. II, 1, p. 83 (1931).

Type : N. Nigeria, Naraguta, *Lely* 725 (K, holotype !).

Observations. — 1. — Also known from Bamenda, British Cameroons (e.g. *Maitland* 1664).

2. — *T. okelensis* var. *okelensis* is known from Senegal, French Guinea, Sierra Leone, Ivory Coast and Ghana (including British Togoland) in W. Africa, and also in Ubangi-Shari and Sudan; it has not, however, yet been found in Nigeria where var. *oblanceolata* occurs.

3. — *T. Pobeguinii* HUTCH. et DALZ. seems to be indistinguishable from *T. okelensis* var. *okelensis*.

Tricalysia okelensis HIERN var. **pubescens** AURÉV. et PELLEGR. ex KEAY, var. nov., a typo ramulis dense puberulis, paginis foliorum inferioribus dense et molliter pubescentibus differt.

Tricalysia okelensis HIERN var. *pubescens* AUBRÉV. et PELLEGR. in AUBRÉV., Fl. For. Soud.-Guin., pp. 466, 468 (1950), descr. gallice tantum.

Tricalysia Pobeguinii HIERN var. *pubescens* AUBRÉV. et PELLEGR. in AUBRÉV., Fl. For. C. Iv. III, p. 242 (1936), descr. gallice tantum.

Type : Ivory Coast, Oumé, *Aubréville* 1261 (P, holotype !).

Tricalysia parva KEAY, sp. nov.; a *T. pallenti* HIERN habitu pumilo, ramulis foliisque glabris, nervis lateralibus paucioribus, inflorescentiis 1-3-floris distinguenda.

Suffrutex circiter 60 cm altus, ramulis glabris virgatis bifariis complanatis instructus. *Stipulae* satis persistentes, in vaginam vix 1 mm longam extra glabram intus pubescentem acuminibus duobus filiformibus 2-4 mm longis coronatam cohaerentes. *Folia* petiolis glabris 1-5 mm longis instructa; lamina papyracea siccitate pallide viridia, elliptica, basi cuneata, apice sensim obtusato-acuminata, 6.5-9 cm longa, 2.5-3.5 cm lata, glabra; costa utrinsecus nervis lateralibus 3-4, in suis axillis nonnunquam foveolatis, instructa; pagina superior costa nervisque vix prominentibus, rete venularum obscuro; pagina inferior costa prominenti, nervis non prominentibus, rete venulatum obscuro. *Inflorescentiae* axillares, sessiles vel subsessiles, 1-3 florae, floribus brevissime pedicellatis; bracteolae calyculiformes, truncato-campanulatae, circiter 1.5 mm altae, extra dense adpresse puberulae. *Calyx* in calyculo sessilis, tubo 2-2,5 mm longo et lobis 4 subulatis 1-1,5 mm longis praeditus, basi tubi glabri excepto extra dense adpresse puberulus. *Corolla* extra glaber, tubo 5 mm longo, intus piloso, lobis 4 oblongis acuminatis, 3,5-4 mm longis et 2 mm latis instructa. *Stamina* filamentis circiter 1,5 mm longis, antheris circiter 3 mm longis instructa. *Ovarium* extra glabrum, biloculare, ovulis pro loculo 2-3. *Stylus* pubescens, circiter 7 mm longus. *Fructus* (*Small* 675) in vivo ceroso-coccineus, ellipsoideus, 3,5-4 mm longus, 3-4 mm latus, extra glaber, calyce persistenti coronatus.

Sierra Leone : (?) Southern Province, Jan. 1908, *C. W. Smythe* 239 (K, holotype). Gola Forest, Bagbe, May 1952, *D. Small* 675 (K, BR), 691 (K, P).

Observations. — 1. — Smythe's specimen has no exact locality, but it probably came from the Southern Province of Sierra Leone, perhaps in the Gola Forest where the same species was found many years later by Small.

2. — Small described this species as « very common » in the rain forest at Bagbe.

Tricalysia Mildbraedii Keay, sp. nov.; a *T. macrophylla* K. Schum. loculis ovarii biovulatis, foliis subtus puberulis distinguenda; a *T. discolore* Brenan, tubo corollae breviore fauce sparse pubescenti, nervis lateralibus paucioribus distinguenda.

Arbuscula usque 8 m alta, ramulis elongatis, internodis 3-6,5 cm longis instructa; ramuli novelli minute puberuli deinde plus minusve

glabrescentes. *Stipulae* satis persistentes, in vaginam 1-2,25 mm longam apice truncatam sed apiculis duobus 1-1,5 mm longis coronatam cohaerentes. *Folia* petiolis 5-7 mm longis juventute minute puberulis praedita; lamina rigide papyracea, anguste elliptica vel oblongo-lanceolata, basi cuneata, apice sensim longe et acute acuminata, 12-20 cm longa, 4,5-6 cm lata; pagina superior nitidula siccitate castanea vel olivacea, glabra, costa nervisque impressis; pagina inferior grisea vel olivacea, costa nervisque prominentibus sparse puberulis, rete venularum satis obvio; costa utrinsecus nervis lateralibus primariis plerumque 7 instructa. *Inflorescentiae* paululo supraäxillares, multiflorae, ad anthesin subsessiles et congestae, minute puberulae; bracteae cupulatim connatae, circiter 1 mm altae, apiculatae; pedicelli ad anthesin brevissimi, sed deinde usque 4 mm elongati, bracteolis 2, ovatis, vix 1 mm longis muniti. *Calyx* 1 mm longus, in 5 lobis ovato-triangularibus profunde divisus, glaber. *Corollae* tubus 3,5-4 mm longus, extra glaber, fauce sparse pubescenti, lobis 5 oblongo-linearibus apice obtusis 3-4 mm longis glabris praeditus. *Stamina* 5, filamentis circiter 1 mm longis, antheris circiter 2 mm longis instructa. *Ovarium* glabrum, biloculare, ovulis 2 pro loculo. *Stylus* glaber, circiter 5 mm longus. *Fructus* (nondum maturus) glaber, ellipsoideo-subglobosus, circiter 4 mm diametro, calyce persistente coronatus.

British Cameroons : Kumba District, Dikome, between Mile 35 and Mile 36 on the Mamfe road, July 1946, *B. J. Akuo* FHI 15158 (FHI, FHO).

French Cameroons : between Yaunde and Dengdeng, 95 km N. E. of Yaunde, Feb. 1914, *J. Mildbraed* 8198 (K, holotype).

Tricalysia obanensis Keay, sp. nov.; a *T. pallenti* Hiern foliis subcoriaceis, nervis lateralibus 3-4(-5) subtus prominentibus, ovulis (3-)4 pro loculo distinguenda.

Planta lignosa, probabiliter frutex vel arbor parva. *Ramuli* juveniles pilis brevissimis dense et molliter vestiti, ei adulti cortice purpureo-brunneo hic illic desquamante obtecti. *Folia* petiolis dense et minute puberulis 3-5 mm longis instructa; lamina firme papyracea vel subcoriacea, discolor, elliptica vel obovato-elliptica, basi cuneata, apice abrupte vel sensim longe obtusato-acuminata, 3,5-8 cm longa, 2-3,5 cm lata; pagina superior siccitate purpureo-brunnea, praeter costam minute puberulam glabra, nervis lateralibus vix conspicuis;

pagina inferior siccitate pallide brunnea, costa et nervis lateralibus prominentibus minute puberulis, ceterum glabra, rete venularum obscuro; costa utrinsecus nervis lateralibus 3-5 instructa. *Inflorescentiae* sessiles vel usque 1 mm pedunculatae, dense puberulae, usque 6-florae; bracteae cupulatim connatae, circiter 1 mm altae, apiculatae; bracteolae calyculiformes, circiter 1 mm altae, biapiculatae. *Calycis* tubus circiter 1,25 mm longus apice truncatus sed dentibus 5 usque 0,25 mm longis coronatus, dense puberulus. *Corollae* tubus 2-3 mm longus, extra glaber, intus pubescens; lobi 5, in alabastrum extra dense pubescentes, anguste oblongi, apice acuti, circiter 3,5 mm longi et 1,25 mm lati. *Stamina* filamentis circiter 0,5 mm longis, antheris circiter 3 mm longis instructa. *Ovarium* glabrum vel apice puberulum, biloculare, ovulis (3-)4 pro loculo. *Stylus* pubescens, circiter 5 mm longus. *Fructus* (nondum maturus) globosus, certe 3 mm diametro, calyce persistenti coronatus.

Eastern Nigeria : Oban District, *Talbot* 1324 (K, holotype).

Observation. — An unnumbered specimen, also collected by the Talbots in Oban and preserved at Kew, is probably conspecific. It has, however, rather larger leaves (up to 12,5 cm long and 4,5 cm broad) and a somewhat different general appearance.

Tricalysia auriculata Keay, sp. nov.; a *T. Chevaliera* K. Krause corolla ante anthesin e calyce tubulari exserta valde distincta; a ceteris speciebus africanis foliis basi cordatis vel auriculatis, venulis parallelis conspicuis, fructibus majoribus, distinguenda.

Planta lignosa, probabiliter frutex vel arbor parva. *Ramuli* dense adpresse hirsuti. *Folia* petiolis 1,3 mm longis more ramulorum vestitis instructa; lamina papyracea, discolor, oblongo-elliptica vel oblongo-obovata, nonnunquam subfalcata, basi inaequaliter anguste cordata vel auriculata, raro subcordata, apice longe acuminata, (5-)12-19,5 cm longa, (2,8-)4-8 cm lata; pagina superior glabra, costa paulo impressa, nervis et venulis parallelis satis obviis; pagina inferior quam superior in sicco pallidior ad costam nervosque prominentes hirsuta, venulis parallelis prominulis valde conspicuis; costa utrinsecus nervis lateralibus (3-)5(-6) adscendentibus submarginem anastomosantibus instructa. *Inflorescentiae* axillares, ut videtur 1-florae; peduncula circiter 3 mm longa, dense adpresse hirsuta; bracteolae calyculiformes tubo circiter 4 mm alto, 4 lobis triangularis circiter 1,75 mm altis et basi 2-2,5 mm latis instructae, extra

pilis brevis intus pilis longis dense adpresse vestitae. *Calyx* in calyculo sessilis, tubo circiter 11 mm longo et 3 mm diametro, dentis 8 vix 0,5 mm longis praeditus, more calyculi vestitus. *Corolla* extra dense adpresse hirsuta, tubo 9 mm longo, intus praesertim in fauce piloso, lobis 8 oblongo-linearibus obtusis circiter 8 mm longis et 3,5 mm latis intus subglabris instructa. *Stamina* 8, filamentis circiter 0,5 mm longis basi antherarum circiter 5 mm longarum affixis instructa. *Ovarium* extra dense adpresse hirsutum, circiter 3 mm longum, biloculare, ovulis pro loculo 4. *Stylus* glaber, circiter 16 mm longus. *Fructus* ellipsoideus basi acutus et hirsutus, apice vestigio calycis hirsuto coronatus, cetere glaber, circiter 3 cm longus et 2 cm diametro, 6-spermus.

Eastern Nigeria : Calabar Province, between Budeng and Ewen Road, near waterside, Nov. 1931, *D. R. Rosevear* C. 33 (K); C. 34 (K, holotype; FHI, isotype).

French Cameroons : Bipinde, 1909, *Zenker* 3860 (BM, K).

Observations. — 1. — The leaves of this species have a superficial resemblance to those of certain species of *Aulacocalyx*.

2. — The corolla is very similar to that of *T. Chevalieri* K. Schum. and other species in that group. These species, however, have the corolla covered by the calyx in bud and at anthesis the calyx splits into 2 or more palaceous pieces. In *T. auriculata* the calyx is tubular, dentate at the apex, and not completely covering the corolla in bud.

3. — I have not found any close affinity for this species.

COFFEA Linn.

Coffea Lemblini (A. Chev.) Keay, comb. nov.

Coffea Lemblini A. Chev., Explor. Bot., p. 336 (1920), nomen nudum.

Randia Lemblini A. Chev., Rev. Bot. Appliq. XVIII, p. 415, t. 10 (1938); Les Caféiers du Globe III, p. 258 (1947).

Type : Ivory Coast, *Chevalier* 17180 (P, holotype !).

Observations. — 1. — Through the courtesy of Prof. Humbert and his staff I have been able to examine the type of this species.

Chevalier did not cite any specimens other than the type which was collected in 1907, nor have I seen any others.

2. — It is difficult to understand why Chevalier changed his mind and eventually described this plant under *Randia*. Each of the two ovary cells has a single ovule attached to the septum, and in many other respects this plant is clearly related to *Coffea Afzelii* Hiern and *C. subcordata* Hiern — species which Lebrun has removed into a separate genus *Argocoffeopsis* Lebrun (1941).

BELONOPHORA Hook. f.

This genus was described by J. D. Hooker, in Hook. Ic. Pl. t. 1127 (1873), as having the ovules solitary and pendulous in each of the two ovary cells. It was, accordingly, assigned to the tribe *Alberteae* by Hooker in his original publication and in Gen. Pl. II, p. 109 (1873), by Hiern in Fl. Trop. Afr. III, p. 129 (1877), by K. Schumann in Engl. et Prantl, Nat. Pflanzenfam. IV, 4, p. 87 (1891) and by Hutchinson and Dalziel in Fl. W. Trop. Afr. II, p. 84 (1931). In the latter work, however, one species — *B. Wernhamii* Hutch. et Dalz. (based on *Diplosporopsis coffeoides* Wernham) — was described as having two ovules in each ovary-cell, thus contradicting the generic key.

I have dissected a flower of the type specimen of Hooker's original species *(B. coffeoides)* and numerous other flowers from other species. In each instance I found a pendulous placenta in each ovary cell, and inserted on the inner side of each placenta I found *two* collateral ovules. I have therefore concluded that the original description and subsequent works were wrong on this point.

Wernham described the new genus *Diplosporopsis* in Cat. Talb. Nig. Pl., p. 47 (1913) and placed it in the *Gardenieae*. He described two species, both of which appear congeneric with *Belonophora*. Wernham described correctly the two ovules collateral in each pendulous placenta, but made no reference to *Belonophora*.

It would be premature for me to assign the genus *Belonophora* Hook. f. [syn. *Kerstingia* K. Schum. (1903) and *Diplosporopsis* Wernham (1913)] to a tribe, since the present classifications are so unsatisfactory. I only wish at this stage to draw attention to the arrangement of the ovules which should exclude *Belonophora* from Hooker's *Alberteae*.

Hutchinson and Dalziel transferred *Diplosporopsis coffeoides* Wernham to *Belonophora*, giving it the new name *B. Wernhamii* because the epithet *coffeoides* was already occupied. They ignored, however, the other species — *Diplosporopsis Talbotii* Wernham — which occurs in the F. W. T. A. area and for which I must now make the new combination, thus :

Belonophora Talbotii (Wernham) Keay, comb. nov.

Diplosporopsis Talbotii Wernham, Cat. Talb. Nig. Pl., p. 47 (1913).

Type : E. Nigeria, Oban, *Talbot* 1056 (BM, holotype !).

Royal Botanic Gardens, Kew.
March 1957.

ESQUISSE D'UNE LIMITE PHYTOGÉOGRAPHIQUE GUINÉO-ZAMBÉZIENNE AU KATANGA OCCIDENTAL

PAR

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Une reconnaissance rapide dans le Katanga occidental nous autorise à préciser quelques limites phytogéographiques de cette région. Nous avons suivi l'itinéraire de Luputa, vers le Sud jusqu'aux sources de la Luilu et Sandoa, pour remonter au Nord vers Kapanga et Mwene-Ditu. (Fig. 27).

Au Nord du 7e parallèle Sud, la végétation est constituée de savanes herbeuses à arbustives, entrecoupées de galeries forestières appartenant aux forêts semi-caducifoliées subéquatoriales et périguinéennes, caractérisées par l'abondance de *Chrysophyllum* sp. (*Liben* 3391), *Marquesia acuminata* (Gilg) R. E. Fries, *Pterygota mildbraedii* Engl., *Celtis zenkeri* Engl., *Carapa procera* DC., *Cathormion leptophylla* (Harms) Keay, *Staudtia stipitata* Warb.

La strate herbacée des savanes contient en abondance *Encephalartos poggei* Aschers., *Smilax kraussiana* Meissn., *Loudetia bequaertii* (De Wild.) C. E. Hubb., tandis que la strate arbustive, à recouvrement très variable, se compose principalement d'espèces à large distribution, de l'ordre des *Hymenocardietalia acidae* et d'espèces zambéziennes assez plastiques dont l'aire de distribution s'étend jusque vers le 6e parallèle : *Hymenocardia acida* Tul., *Maprounea africana* Muell. Arg., *Erythrophleum africanum*

(Welw.) Harms, *Entadopsis abyssinica* (Steud. ex A. Rich.) Gilbert et Boutique, *Combretum laxiflorum* Welw., *Combretum kwinkitii* De Wild., *Terminalia mollis* Laws, *Piliostigma thonningii* (Schum.) Milne-Redhead, *Dialium englerianum* Henriques, *Parinari mobola* Oliv.

Notons, en outre, la présence de forêts tropophiles à *Berlinia giorgii* et *Uapaca nitida*. Elles constituent généralement de petits boqueteaux en bordure des galeries forestières, plus rarement isolés dans la savane.

Ces deux espèces pénètrent à l'intérieur des galeries pour former des forêts mixtes, en association avec *Marquesia acuminata* (Gilg) R. E. Fries et des espèces forestières typiquement guinéennes.

Signalons également la présence sporadique jusqu'au Nord du 7e parallèle, de *Brachystegia spiciformis* Benth. en bordure de certaines galeries. Entre les 7e et 8e parallèles Sud, cette espèce constitue fréquemment, en lisière des galeries, des peuplements presque monophytiques.

Berlinia giorgii devient de plus en plus abondant à mesure que l'on s'avance vers le Sud, tandis que *Hymenocardia acida* et *Entadopsis abyssinica* se font plus rares. Le caractère zambézien de la végétation s'accentue dès que l'on s'avance au Sud du 8e parallèle, sur les formations sableuses du Kalahari, vers 1.000-1.100 m d'altitude. Les chaméphytes deviennent extrêmement abondants dans les savanes en même temps qu'apparaissent certaines espèces nettement liées aux forêts claires tropophiles, telles que *Brachystegia longifolia* Benth. Signalons l'abondance locale de *Boophone disticha* (L. f.) Herb.

A l'Ouest de Kapanga, nous retrouvons, sur sable du Kalahari, des savanes densément arbustives où abondent *Erythrophleum africanum* (Welw.) Harms, *Dialium englerianum* Henriques, *Combretum* div. sp., *Pterocarpus angolensis* DC., *Entadopsis abyssinica* (Steud. ex A. Rich.) Gilbert et Boutique, *Terminalia mollis* Laws et, accessoirement, *Berlinia giorgii* De Wild.

De petits boqueteaux, dominés par *Daniella alsteeniana* Duvigneaud, abritent diverses espèces de forêt claire tropophile en voie de dégradation : *Pseudolachnostylis maprouneifolia* Pax, *Combretum mechowianum* O. Hoffm., *Swartzia madagascariensis* (Taub.) Desv. Ces mêmes espèces se retrouvent d'ailleurs dans la strate arbustive des savanes tandis que la strate herbacée est dominée par des graminées et comporte peu de chaméphytes.

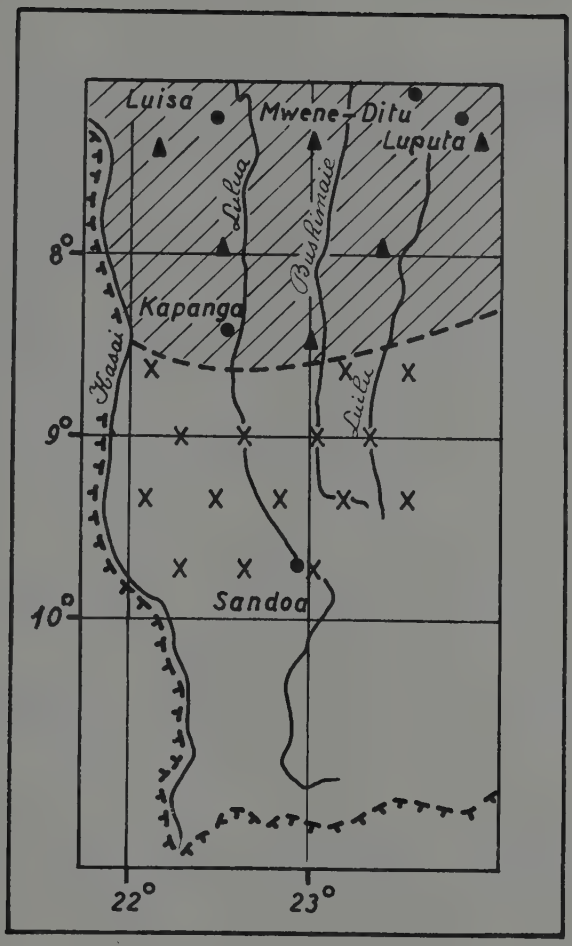

Fig. 27.

Limite guinéo-zambézienne.

Savanes arbustives guinéo-zambéziennes et galeries forestières périguinéennes.

Forêts tropophiles à *Berlinia giorgii* et *Uapaca nitida*.

Forêts tropophiles à *Brachystegia longifolia* et *Syzygium benguellense;* savanes à chaméphytes.

Ce caractère, joint au fait que les espèces arbustives susmentionnées remontent assez loin vers le Nord (jusqu'au 6e parallèle Sud) dans les savanes de la région guinéenne, nous amène à considérer ces savanes non pas comme un stade de dégradation des forêts tropophiles, mais comme une pénétration vers le Nord d'éléments zambéziens, à la faveur de la disparition de forêts à caractère plus hygrophile et ce, probablement, sous l'influence de facteurs anthropiques.

Plus vers le Sud, nous trouvons, un peu au Nord du 9e parallèle, d'authentiques forêts tropophiles de l'alliance du *Berlinio-Marquesion*. Elles sont dominées, physionomiquement, tantôt par *Julbernardia paniculata* (Benth.) Troupin, tantôt par *Brachystegia longifolia* Benth. et diverses autres espèces, ce dernier cas étant le plus fréquent.

Les diverses strates se répartissent comme suit :

— Une strate supérieure arborescente de 15 à 25 m et recouvrant 60 à 70 % de la surface.
— Une strate arbustive supérieure de 5 à 10 m, recouvrant 30 à 60 %.
— Une strate arbustive inférieure de 1 à 5 m, recouvrant 50 %.
— Une strate herbacée discontinue, à recouvrement très variable suivant le degré de dégradation du groupement.
— Quelques lianes.

La plupart des espèces, au moins parmi les dominantes, sont tropophiles; en fin de saison sèche, les jeunes feuilles pendantes et vivement teintées de rouge confèrent à ces forêts un aspect très particulier.

Citons parmi les espèces constantes ou qui semblent caractéristiques :

1) Espèces à distribution zambézienne :

Brachystegia longifolia Benth., *Combretum zeyheri* Sond., *Strychnos cucculoïdes* Bak., *Diplorrhynchus angolensis* Buttn., *Guibourtia coleosperma* (Benth.) J. Leonard, *Landolphia camptoloba* (K. Sch.) M. Pichon, *Afzelia cuanzensis* Welw., *Monotes* cfr *caloneurus* Gilg (*Liben* 3816), *Ochna hoffmannii-ottonis* Engl., *Paropsia brazzeana* Baill., *Pseudolachnostylis maprouneifolia* Pax, *Scleria nyasensis* C. B. Clarke, *Strychnos malaco-*

clados Wright, *Toxocarpus brevipes* N. E. Br., *Uapaca* sp. (*Liben* 3769), *Uapaca* sp. (*Liben* 3798), *Uapaca* sp. (*Liben* 3773), *Ancylanthus fulgidus* Welw. et Hiern., *Rauvolfia nana* E. A. Brenan, *Garcinia* cfr *huillensis* Welw. ex Oliv. (*Liben* 3790).

2) Espèces à distribution guinéenne ou espèces de liaison :

Chaetocarpus africanus Pax, *Xylopia staudtii* Engl. et Diels, *Diospyros* sp. (*Liben* 3791), *Gaertnera paniculata* Benth., *Leptoderris nobilis* (Welw. ex Bak.) Dunn., *Oxyanthus speciosus* DC.

3) Espèces plus particulièrement caractéristiques des forêts semi-caducifoliées périguinéennes :

Cathormion leptophylla (Harms) Keay, *Marquesia acuminata* (Gilg) R. E. Fries, *Syzygium benguellense* (Welw. ex Hiern) Engl., *Staudtia stipitata* Warb.

4) Espèces guinéennes qui, sans être particulièrement abondantes, mettent en évidence une forte influence guinéenne :

Artabotrys likimensis De Wild., *Dichapetalum thonneri* De Wild., *Dichapetalum lujae* var. *brevipile* Hauman, *Carinta obvallata* (Didr.) Tayl., *Manotes pruinosa* Gilg, *Ongokea gore* (Hua) Pierre, *Alchornea cordifolia* Muell. Arg.

Le tableau ci-dessous donne les coefficients d'abondance-dominance de quelques espèces dans trois placeaux différents :

	1	2	3
Albizzia adianthifolia	+	—	+
Brachystegia longifolia	5 ?	3.1	2.1
Carinta obvallata	2.1	—	—
Centhotheca mucronata	2.3	2.3	+
Chaetocarpus africanus	3.1	3.1	3.1
Combretum zeyheri	2.1	3.1	—
Dalbergia lactea	2.1	3.1	+
Daniellia alsteeniana	—	—	3.1
Diospyros sp. (herb. *Liben* 3791)	+	2.1	+
Diplorrhynchus angolensis	2.1	3.1	1.1
Erythrophleum africanum	—	3.1	+

Gaertnera paniculata	2.1	—	2.1
Garcinia cfr *huillensis* (herb. *Liben* 3790) ...	—	+	+
Hymenocardia ulmoides [1]			
Landolphia camptoloba	2.2	2.2	+
Leptoderris nobilis	—	—	1.1
Ochna hoffmanni-ottonis	—	+	+
Pseudolachnostylis maprouneifolia	+	2.1	+
Pterocarpus angolensis	+	3.1	+
Scleria nyasensis	1.2	2.3	1.3
Syzygium benguellense	2.1	+	3.1
Uapaca sp. (herb. *Liben* 3769)	2.1	—	2.1
Uapaca sp. (herb. *Liben* 3773)	+	—	—
Uapaca sp. (herb. *Liben* 3798)	—	2.1	—
Xylopia staudtii	—	2.1	3.1

Ces forêts présentent divers stades de dégradation et aboutissent à des savanes arbustives où abondent les chaméphytes :

Ochna gracilipes Hiern, *Mechovia grandiflora* Schinz, *Polycarpaea poggei* Pax, *Oxygonum dregeanum* var. *wittei* (Staner) R. Grah., *Helichrysum* sp. (*Liben* 3823), *Vernonia* sp. (*Liben* 3825) et parmi les graminées : *Loudetia* cfr *angolensis* C. E. Hubb. (*Liben* 3772) et *Rhynchelytrum amethysteum* (Franch.) Chiov., tandis que la strate arbustive est dominée par *Erythrophleum africanum;* y sont associés : *Albizzia versicolor* Welw. ex Oliv., *Albizzia antunesiana* Harms, *Isoberlinia niembaensis* (De Wild.) Duvign., *Sterculia quinqueloba* Harms, *Maprounea africana* Muell. Arg., *Swartzia madagascariensis* (Taub.) Desv., *Berlinia giorgii* De Wild., *Diplorrhynchus angolensis* Büttn.

Pour autant que nous ayons pu en juger au cours d'un voyage aussi rapide, ces savanes à chaméphytes couvrent des surfaces bien plus importantes que les forêts tropophiles.

Ces deux types de végétation sont exclusivement liés aux sables du Kalahari.

Les vallées encaissées abritent des galeries forestières à caractère guinéen tandis que les plaines alluviales, inondées pendant une bonne partie de l'année, sont occupées par des savanes herbeuses paludicoles (Desenfans, 1950).

[1] Dans les trois placeaux, cette espèce montre une vitalité réduite.

Conclusions.

Le Katanga occidental se situe, au point de vue phytogéographique (Duvigneaud, 1950), dans la Région soudano-zambézienne, Domaine zambézien, Secteur lundien, District du Katanga occidental.

Ce district est limité au Nord par le district transitoire du Lomami, appartenant à la Région guinéenne, et caractérisé dans sa partie méridionale par : des savanes généralement arbustives à caractère guinéo-zambézien, des galeries forestières périguinéennes et des forêts tropophiles à *Berlinia giorgii* et *Uapaca nitida*. Ainsi définie, cette portion méridionale constitue une transition guinéo-zambézienne et doit être séparée de la partie Nord, à caractère nettement guinéen.

Quant aux forêts tropophiles décrites ici, elles accusent un très net caractère zambézien, tempéré toutefois par la présence de nombreuses espèces guinéennes ou de liaison, relictes d'une forêt plus hygrophile et subtropophile, probablement apparentée à l'association à *Marquesia acuminata* et *Pteleopsis diptera* Devred (1958).

Nous proposons de faire coïncider la limite de la Région guinéenne et du Domaine zambézien avec la limite septentrionale de leur aire de distribution.

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ÜBER EINIGE KONGOLESISCHE *AEOLANTHUS*-ARTEN

VON

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Aeolanthus zählt zu jenen drei Labiaten-Gattungen, deren Kelche zur Zeit der Samenreife mittels einer transversalen, in sich zurücklaufenden Dehiszenzlinie eine Art Deckel abgliedern. Die Zirkumzissur zeigt gewöhnlich einen kreisförmigen Verlauf (Abb. 28). Bei einigen Arten verhält sie sich jedoch insofern abweichend, als sie dort geschwungen ist, was zur Folge hat, dass sowohl der basale Kelchnapf wie auch die abfallende Kelchhaube streng dorsiventrale Gebilde darstellen (Abb. 29). Auf die morphologischen und verbreitungsbiologischen Verhältnisse dieser Art wird an anderer Stelle eingegangen (Stopp 1958).

In der taxonomischen Literatur ist die dorsiventrale Öffnungsweise der Deckelkelche kaum gewürdigt worden, obgleich ihr sehr prägnante, auch an Herbarmaterialien recht leicht feststellbare Strukturen zugrunde liegen. Zumindestens bei drei verschiedenen Artengruppen scheint diese Gestaltung aufzutreten. Dem Verf. standen die reichen Kongo-Materialien des Brüsseler Staatsherbars zur Verfügung, die wegen ihrer guten Erhaltung sichere morphologische Analysen zuliessen (1).

(1) Herrn Prof. Dr. W. Robyns danke ich aufrichtig für die grosszügige leihweise Überlassung selbst des Typenmaterials, Herrn E. Petit für die Sichtung der noch ungeordneten Bögen.

Während der Studien erwies sich die herkömmliche Gliederung der teilweise unübersichtlichen Gattung als unbefriedigend. Die Einteilung von Briquet beruht zum grossen Teil auf irrigen Prämissen, so dass sie nicht aufrecht erhalten werden kann. So zeigt sich, dass die Infloreszenz bei *Aeolanthus* recht gleichförmig gebaut ist. Sowohl die Endinfloreszenz wie auch die Bereicherungssprosse

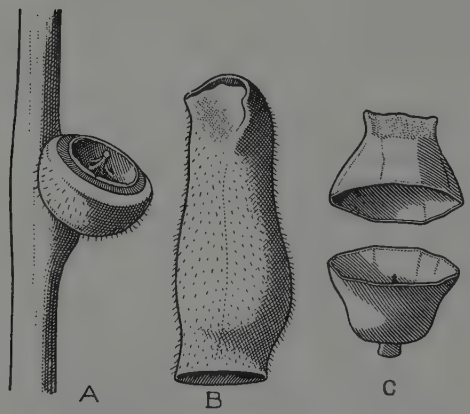

Abb. 28. — *Aeolanthus rehmannii* Gürke: A und B, basaler und apikaler Teil des dehiszierten Kelches; *A. pinnatifidus* Hochst.: C, dehiszierter Kelch.

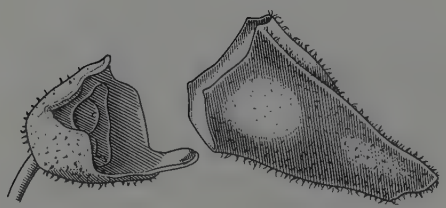

Abb. 29. — *Aeolanthus virgatus* Gürke: dehiszierter Kelch.

wachsen monopodial, sind also im Gegensatz zu der Angabe von Briquet nicht zymös gebaut. Sie täuschen dem flüchtigen Beobachter freilich wickelige Verzweigung vor. So ist stets nur eines der beiden dekussiert stehenden Hochblätter fertil und trägt eine Blüte. Dabei ändert sich die Fertilität nicht spirodom; vielmehr stehen die blütentragenden Brakteen der entsprechenden Wirtel superponiert. Dem Gesetz der Alternanz zufolge resultieren also bei der Dekussation zwei fertile und zwei sterile Orthostichen von Hoch-

blättern, ein Verhalten, das sich auch bei anderen Familien, etwa den Acanthaceen, vorfindet. Innerkalb der Labiaten freilich scheint es einzigartig zu sein. Die verwandten Gattungen der *Plectranthinae*, zu denen *Aeolanthus* schon auf Grund des Blütenbaues und der sternotriben Bestäubungsweise gehört, zeigen andere Verhältnisse (Abb. 30).

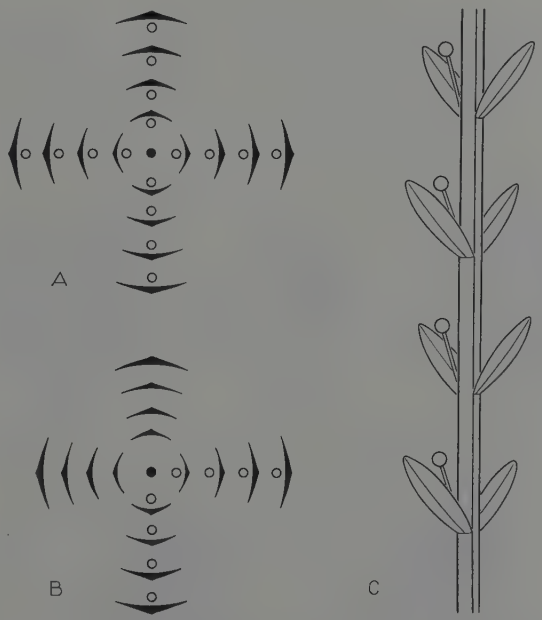

Abb. 30. — *Coleus arabicus* BENTH.: A. Diagramm der Infloreszenz; *Aeolanthus virgatus* GÜRKE: B. Diagramm der Infloreszenz; C. Blütenanordnung (s. Text).

Im Gegensatz zu der verwandten Gattung *Coleus* (Abb. 30 A), dessen Infloreszenzen radiär gebaut sind, zeigen die von *Aeolanthus* somit eine ausgeprägte Dorsiventralität. Die äussere Ähnlichkeit mit einer Wickel wird weiter durch die Tatsache betont, dass die Infloreszenzen spitzenwärts eingekrümmt sind, wobei die geförderte, blütentragende Seite nach oben gekehrt ist. Auch verstärkt sich postfloral die Einseitswendigkeit, indem sich die persistierenden Kelche durch Torsionen mehr oder minder in eine Reihe einordnen.

Schliesslich sind die fertilen Brakteen hinfälliger als die sterilen, weshalb sich bei vielen Arten zur Zeit der Samenreife nur noch letztere an der Fruktifizenz vorfinden. Auch durch dieses Verhalten wird eine wickelige Verzweigung vorgetäuscht.

Die Ausbildung der dorsiventral dehiszierenden Fruchtkelche korrespondiert in der Weise mit der Wuchsform der betreffenden Arten, dass sich drei Gruppen unterscheiden lassen. Die eine wird von der sehr variablen *A. virgatus* bestritten, die andere stellt den Artenkreis um *A. stormsii* dar. Die letzte schliesslich, die in der vorliegenden Untersuchung infolge zu geringen Vergleichsmaterials nicht berücksichtigt werden kann, besitzt die extremsten Kelchformen (Abb. 31 D, E).

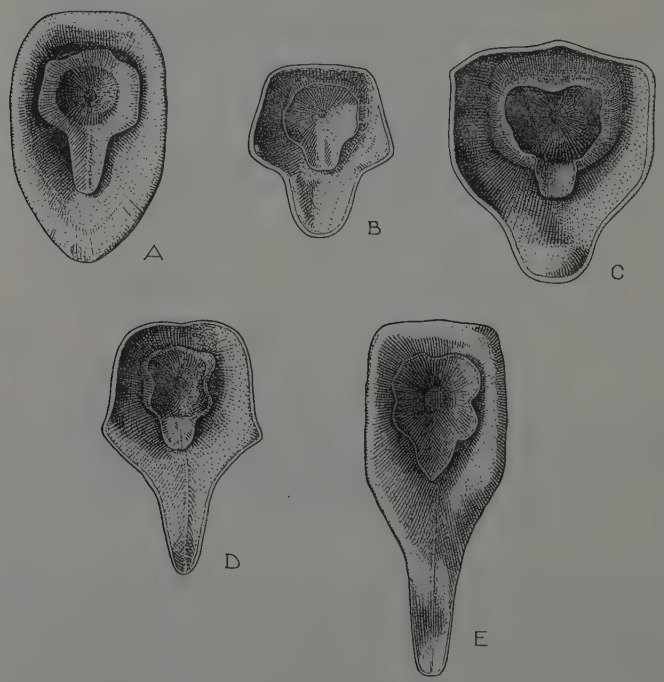

Abb. 31. — Aufsicht auf die nach der Dehiszenz an der Mutterpflanze verbleibenden Kelchnäpfe; bei der inneren Struktur handelt es sich um die manschettenartigen Reste der Blütenkrone : A. *Aeolanthus stormsii* Gürke; B. *A. stormsioides* Stopp; C. *A. virgatus* Gürke; D. *A.* spec. (*Germain* 6795); E. *A.* spec. (*Germain* 6290).

Aeolanthus virgatus Gürke, Engl. Bot. Jahrb., XXII, p. 146 (1895).

Oubangi-Chari : Haut Chari, Kaga Mbra, 29-11-1902, *Chevalier* 6446 (BR) (fruchtend). — Abb. 32 A.

Congo Belge : Uele, Strasse zwischen Bambesa und Ango, Höhe 600 m, 13-11-1945, *Germain* 4276 pro parte (BR) (fruchtend).

A B

Abb. 32. — A. *Aeolanthus virgatus* Gürke (*Chevalier* 6446); B. *A. virgatus* var. *foliosus* Stopp (*Gérard* 1876).

Infolge ihres grossen Verbreitungsareals variiert diese Art habituell ausserordentlich. Zwischen gestaucht wachsenden Pflanzen (30 cm) und laxen Exemplaren von 70 cm Höhe gibt es alle Übergänge. Von den anderen Arten mit dehiszierenden Fruchtkelchen

distanziert sich die Art durch schmal lineare, etwas sukkulente Blätter, deren Ränder nach unten ein wenig eingerollt sind.

Die Hochblätter werden im Verlaufe der Postfloration hinfällig wobei die sterilen etwas länger erhalten bleiben. Bie beiden Orthostichen von Fruchtkelchen schieben sich im Verlaufe der Reife ineinlander, mit dem Erfolg, dass die Fruktifizenz streng einseitswendig wird. Auffällig ist bei der typischen Form der geringe vegetative Unterbau des Primärsprosses wie auch der das Bereicherungssprosse. Bei den letzteren, die in ihren Aufbau den des Primärssprosses wiederholen, tragen häufig bereits die Vorblätter Sprosse dritter Ordnung. Dabei gleicht die Verzweigung der Bereicherungssprosse wie auch die des Primärsprosses sptizenwärts den Verhältnissen, die sich in den Infloreszenzen selbst vorfinden. Jeweils nur eines der beiden Blätter eines Wirtels wird zum Tragblatt. Die Fertilität aufeinander folgender Wirtel verschiebt sich dabei nicht spirodrom.

Im Generativen erweist sich die Art als überhaus einheitlich. Lediglich die Hochblätter variieren in Gestalt nud Haarbesatz beträchtlich.

Aeolanthus virgatus Gürke var. **foliosus** Stopp var. nov. — Abb. 32 B.

Variatio flore et fructu speciei similis sed in habitu valde differens. Supra ramis basalibus caulis primarius 7 usque 12 vertices foliorum sterilium ferens.

Congo Belge: Tukpwo, Savanne, 10 Okt. 1955, *Gérard* 1876 (Holotypus BR) (blühend und fruchtend); id., Pengbele, 11 Sept. 1954, *Gérard* 1745 (BR) (blühend und fruchtend).

Im Generativen gleicht die Varietät vollständig der Hauptart. Sie unterscheidet sich aber beträchtlich in der Wuchsform und hier in einem Mass, dass ihr vielleicht sogar Artrang zugeschrieben werden muss. Auch bei dieser Form ist der vegetative Unterbau des Primärsprosses gering. Auf eine Zone von Bereicherungssprossen folgt nun aber nicht die Infloreszenz, es ist vielmehr eine Hemmungszone dazwischengeschaltet, die 7-12 Wirtel steriler Blätter umfasst. Erst dann folgen Partialinfloreszenzen. Bei den Bereicherungssprossen wiederholt sich dieser Aufbau.

Aeolanthus stormsii GÜRKE, Bull. Herb. Boiss., IV, p. 820 (1896).

TANGANYIKA : Karema, *Storms* 13 (Typus BR).

Bei dieser annuellen Art wie auch bei der folgenden fällt die starke Anisophyllie der Hochblätter auf. Während diejenigen Blattorgane eines Wirtels, die eine Blüte hervorbringen, breit obovat gestaltet sind, zeigen die sterilen jeweils eine lanzettliche Form. Beide Orthostichen von Blüten sind auch zur Zeit der Fruchtreife gut zu erkennen.

Die schräg orientierte Dehiszenzlinie am Fruchtkelch verläuft geradlinig, so dass der stehenbleibende Basalteil des Kelches einen glatten Rand aufweist. In diesem Merkmal unterscheidet sich diese Art eindeutig von der folgenden.

Aeolanthus stormsioides STOPP sp. nov.

Annuus, in habitu *A. stormsii* affinis; caulis e base ramosissima. Bracteae forma magnitudineque differens, fertiles late obconici, steriles lanceolati. Calyx tempore maturitatis seminum circumcissione dehiscens. Labiae calycis aequilongae, claudentes. Cupula persistens calycis cum labia abaxiale et dentibus transversalibus.

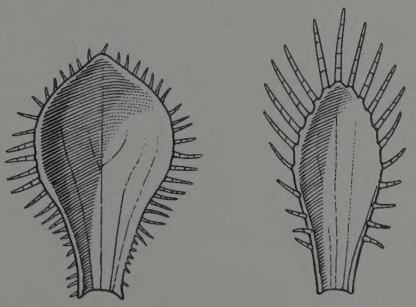

Abb. 33. — *Aeolanthus stormsioides* STOPP : links fertile, rechts sterile Braktee.

CONGO BELGE : Sandoa, in feuchtem Humus von Granitspalten, April 1931, *Overlaet* 1256 (Holotypus BR) (blühend und fruchtend); Kaniama, Haut Lomami, 24°30' O. 70°30' W., Höhe 900 m, in Spalten von Granitfelsen, 20-4-1947, *Mullenders* 289bis (BR) (fruchtend); id., gleicher Standort, Blüten rosa, 10-4-1947, *Mullenders* 290bis (BR) (blühend und fruchtend).

Diese Art ist habituell der vorigen ausserordentlich ähnlicht, Auch in der Blütenform lassen sich keine wesentlichen Unterschiede finden. Die Hochblätter sind ebenfalls in der gleichen Weise anisophyll (Abb. 33).

Der wesentliche Unterschied liegt im Dehiszenzmodus der Fruchtkelche. Die Trennungslinie verläuft bei dieser Art geschwungen, so dass die Kelchkupula einen ausgerandeten Saum aufweist. Neben einer median abaxialen Lippe finden sich an der persistierenden Kelchbasis zwei seitliche Ausbuchtungen. Dieses Merkmal gestattet die beiden Arten leicht voneinander zu trennen.

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TABLE DES MATIERES | INHOUDSTAFEL

B. VERDCOURT. — Remarks on the classification of the *Rubiaceae* (pl. VIII-XVI) 209

R. W. J. KEAY. — Notes on *Rubiaceae* for the « Flora of West Tropical Africa » — II 291

L. LIBEN. — Esquisse d'une limite phytogéographique guinéo-zambézienne au Katanga occidental (fig. 27) 299

K. STOPP. — Über einige Kongolesische *Aeolanthus*-Arten (fig. 28-33) 307

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